

**Proceedings
of
XV International
Congress of Entomology**



**Washington, D. C.
August 19-27, 1976**

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**Proceedings
of
XV International
Congress of Entomology**



**Washington, D. C.
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TABLE OF CONTENTS

REPORT ON THE CONGRESS.	1
MEMBERS OF THE CONGRESS	9
OPENING PLENARY SESSION REMARKS	31
FINAL PLENARY SESSION REMARKS	33
RESOLUTION AND ANNOUNCEMENTS SUBMITTED BY THE PERMANENT COMMITTEE	33
IN REMEMBRANCE	34
OPENING PLENARY SESSION ADDRESS: Entomology and Mankind. T. R. E. SOUTHWOOD	36
CLOSING PLENARY SESSION ADDRESS: Entomology and the Problems of the Tropical World T. R. ODHIAMBO	52

Section 1: Systematics

THE DIVERSITY OF INSECTS AND THE DOMINANCE OF THE LAND

Geological History and Evolution of the Insects FRANK M. CARPENTER	63
Enabling Mechanisms H. E. HINTON	71
Why Are There So Many Species of Insects? DANIEL H. JANZEN	84

Section 2: Genetics

GENETIC CONTROL OF INSECTS

Meiotic Drive and Sex Ratio Distortion in the Mosquito <i>Aedes aegypti</i> R. J. WOOD AND M. E. NEWTON	97
Testing Systems for the Genetic Control of Mosquitoes C. F. CURTIS	106
Genetic Manipulation of <i>Aedes aegypti</i> . II. A Cytogenetic Study of Radiation Induced Translocations in DELHI Strain E. HALLINAN, NANCY LORIMER, AND K. S. RAI	117
Current Status of Genetic Control of the Australian Sheep Blowfly, <i>Lucilia cuprina</i> (Wiedemann) (Diptera; Calliphoridae) M. J. WHITTEN, G. G. FOSTER, W. G. VOGT, R. L. KITCHING, T. L. WOODBURN, AND C. KONOVALOV	129
Isozyme Variability Studies of Translocation Homozygotes in the House Fly, <i>Musca domestica</i> L. IAN C. MCDONALD AND ODELL A. JOHNSON	140
The Application of Compound Autosomes to Insect Control Including the First Experimental Successes with Compound-Fragment Combinations M. FITZ-EARLE AND D. G. HOLM	146
Current Status of Genetic Control of Hessian Fly Populations With the Dominant Great Plains Race J. E. FOSTER	157

Section 3: Physiology and Biochemistry

INSECTS IN EXTREME ENVIRONMENTS

Insects in the High Arctic JAMES K. RYAN	167
Distribution and Isolating Factors in the Races of <i>Papilio machaon</i> (Lepidoptera: Papilionidae) in Central Himalaya. WOLFGANG DIERL	171

Strategies of Low Temperature Adaptation JOHN G. BAUST AND R. E. MORRISEY 173

Altitude- and Time-related Changes in Arthropod Faunation (Central High Alps:
Obergurgl-area, Tyrol)
H. JANETSCHEK, I. DE ZORDO, E. MEYER, H. TROGER, AND H. SCHATZ 185

Section 3: Physiology and Biochemistry,
Section 5: Ecology, and
Section 8: Biological Control.

PHYSIOLOGY AND BIOCHEMISTRY OF INSECT/HOST INTERACTIONS

The Role of Chemical Factors in Insect/Plant Relationships.MARCOS KOGAN 211

Sensory Aspects of Insect Plant Interactions.ERICH STAEDLER 228

The Effect of Plant Secondary Products on Insect Plant Co-evolutionT. SWAIN 249

The Physiology of Hematophagous Insect/Animal Host Relationships RACHEL GALUN 257

Chemical Exchanges Between the Mouth Parts of Ticks and Their HostsJ. E. O'HAGAN 266

Physiology and Biochemistry of Insect Host Interactions:
ConclusionsL. M. SCHOONHOVEN 277

Section 6: Behavior
PHEROMONES, ALLOMONES, AND KAIROMONES:
THEIR SIGNIFICANCE IN INSECT BIOLOGY

Evolutionary Aspects in Chemical Ecology and
Chemical Communication JACQUES M. PASTEELS 281

The Adaptiveness of Pheromone Communication H. H. SHOREY 294

Aspects of Nervous Coding of Sensory Quality in the Olfactory Pathway
of Insects. JURGEN BOECKH 308

Arthropod Allomones: Chemical Effronteries and AntagonistsS. S. DUFFEY 323

Section 7: Social Insects and Apiculture
COMMUNICATION AND LEARNING IN SOCIAL INSECTS

Learning and CommunicationHUBERT MONTAGNER 397

Some Aspects of Communication in TermitesALASTAIR M. STUART 400

Acoustical Communication in Wasp Colonies (Vespinae). JACOB ISHAY 406

Egg Laying, Aggression and Dominance in Bees.H. H. W. VELTHUIS 436

Recent Advances in the Orientation and Learning of Honeybees.MARTIN LINDAUER 450

Section 8: Biological Control
MODERN ACHIEVEMENTS AND INNOVATIONS IN BIOLOGICAL CONTROL

Modern Achievements and Innovations in Biological Control L. E. CALTAGIRONE 463

Biological Control of Agricultural Pests F. J. SIMMONDS AND F. D. BENNETT 464

Microbial Control of Arthropod Pests T. A. ANGUS 473

Biological Control of Weeds: From Art to Science PETER HARRIS 478

Section 9: Medical and Veterinary Entomology
CHANGING PATTERNS IN THE TRANSMISSION
OF ARTHROPOD-BORNE DISEASES

The Ecology of Chigger-borne Rickettsiosis and Murine Typhus—Changing Concepts and Epidemiology	ROBERT TRAUB, CHARLES L. WISSEMAN, JR., AND ABDULRAHMAN FARHENG-AZAD	487
Changes in the Epidemiology of Dengue and the Emergence of Dengue Hemorrhagic Fever	JOHN E. SCANLON	490
Recent Changes in the Epidemiology of Bancroftian Filariasis	BOTHA DE MEILLON	498
New World Leishmaniasis: A Review of the Epidemiological Changes in the Last Three Decades	R. D. WARD	505
Recent Changes in the Epidemiology of Malaria	RONALD A. WARD	523
Anthropogenous Influence on the Existence of Natural Foci of Diseases	V. CERNY AND B. ROSICKY	530

Section 10: Agricultural Entomology and Pest Management
SYSTEMS APPROACH TO PEST MANAGEMENT

The Strategy and Tactics of Integrated Pest Management	G. MATHYS	535
The Utility of Systems Analysis Techniques in Pest Management and Crop Production	GORDON R. CONWAY	541
New Systems Technology for Cotton Production and Pest Management.	A. P. GUTIERREZ, D. W. DEMICHELE, AND Y. WANG	553
The Ecological Basis of Biological Control	C. B. HUFFAKER, R. F. LUCK, AND P. S. MESSENGER	560
Implementation and Economic Returns from the Systems Approach to Pest Management in Cotton	RAY FRISBIE	587
Systems Approach for Management of Rice Pests	KEIZI KIRITANI	591

Section 10: Agricultural Entomology and Pest Management;
Section 8: Biological Control; and,
Section 5: Ecology.

NATURAL FACTORS REGULATING PEST POPULATIONS

The Potential for Manipulating Natural Control Factors for Plant Diseases	KENNETH F. BAKER	601
Some Practical Implications of Recent Theoretical Studies of Host-Parasitoid Interactions	M. P. HASSELL	608
Natural Control Factors Operating in Some European Forest Insect Populations	W. BALTENSWEILER	617
Natural Factors Operating in the Population Dynamics of <i>Heliothis zea</i> in North Carolina	R. E. STINNER, R. L. RABB, AND J. R. BRADLEY, JR.	622
The Role of Pheromones in the Population Dynamics of the Western Pine Beetle	DAVID L. WOOD AND WILLIAM D. BEDARD	643

Section 11: Forest Entomology

INSECT IMPACTS ON THE QUALITY OF FOREST AND URBAN ENVIRONMENTS

Insect Impact on the Quality of Forest and Urban Environments:

The Biological Viewpoint VIKTOR BUTOVISCH 655

Insect Impacts on the Quality of Forest and Urban Environments:

The Economic Viewpoint ROBERT MARTY 661

Section 12: Stored Products and Structural Insects

TROPICAL STORED-PRODUCT ENTOMOLOGY

Tropical Stored-Product Entomology: Introduction PETER F. PREVETT 671

Tropical Storage Entomology and the Small Farmer. T. AJIBOLA TAYLOR 673

Distribution and Abundance of Insects in Butyl-Rubber/EPDM

Silos Containing Wheat. S. NAVARRO 680

The Potential for Use of Synthetic Sex Pheromones for Control of

Ephestia Cautella in Tropical Countries C. P. HAINES 688

Pests of Stored Beans and Their Economic Importance

in Latin America A. V. SCHOONHOVEN 691

An Ecological Study of Traditional On-Farm Maize Storage in Kenya

and the Effects of a Control Action C. P. F. De LIMA 699

Action Versus Its Justification: Which Comes

First? H. R. SHUYLER, G. G. CORBETT, E. REUSSE, AND W. BARREVELD 705

Section 13: Pesticide Development, Management and

Regulation; and Section 4: Toxicology

PESTICIDE DEVELOPMENT

Pesticide Development: Introductory Remarks. RICHARD BACK 711

Pesticide Development—Sociological and Etiological

Background CARL DJERASSI 712

The Evolution of Pesticides and the

Philosophy of Regulation FREDERICK W. WHITEMORE 714

Hazards of Pesticide Development and Mammalian Toxicity:

Carcinogenicity, Teratogenicity, and Mutagenicity. MORRIS F. CRANMER 719

Pesticide Developments and the Question of Side Effects and

Environmental Hazards. H. GYSIN 737

Pesticide Development and Needs in Developing Countries A. V. ADAM 741

Pesticide Development and the Chemical Manufacturer. J. T. BRAUNHOLTZ 747

Section 13: Pesticide Development, Management, and

Regulation; and Section 4: Toxicology

PESTICIDE RESISTANCE I*

Pesticide Resistance as an Evolutionary Phenomenon G. P. GEORGHIOU 759

FAO Activities in the Field of Pesticide Resistance D. F. WATERHOUSE 786

Problems of Resistance in Pests of Field Crops H. T. REYNOLDS 794

Problems of Insecticide Resistance in Insect Vectors of Human Disease R. PAL 800

Pesticide Management on a Major Crop with Severe Resistance

Problems MARIO A. VAUGHAN AND GLADYS LEON Q. 812

Epilogue: Resistance as a Factor in Pesticide Management A. W. A. BROWN 816

*Ed. Note: The Symposium entitled Pesticide Resistance II, given on Monday, August 23, will be published in a separate volume by Academic Press.

REPORT ON THE CONGRESS

By George Anastos, Secretary General

The XVth International Congress of Entomology was held in Washington, D.C., August 19-27, 1976, at the Washington Hilton Hotel. The Congress was sponsored by the Entomological Society of America.

The membership of the Congress consisted of Full Members, Student Members, and Associate Members. Although a total of 2428 individuals was enrolled in the Congress, the total number actually in attendance at the Congress was 2315 individuals from 72 countries.

The enrollment according to categories of membership was: Full Members — 1775; Student Members — 361; and Associate Members — 292.

The actual attendance at the Congress according to categories of membership was: Full Members — 1693; Student Members — 344; and Associate Members — 278.

The countries represented at the Congress were: Algeria, Argentina, Australia, Austria, Bangladesh, Belgium, Bermuda, Bolivia, Brazil, Canada, Canal Zone, Chile, Colombia, Czechoslovakia, Denmark, Egypt, El Salvador, Ethiopia, Finland, France, Germany, East, Germany, West, Ghana, Greece, Honduras, Hong Kong, Hungary, India, Indonesia, Iran, Iraq, Ireland, Israel, Italy, Japan, Kenya, Korea, Kuwait, Liberia, Libyan Arab Republic, Malaysia, Mexico, Morocco, Netherlands, New Zealand, Nicaragua, Nigeria, Norway, Pakistan, Papua New Guinea, Philippines, Poland, Republic of South Africa, Rhodesia, Romania, Spain, Surinam, Sweden, Switzerland, Taiwan, Tanzania, Thailand, Turkey, Uganda, United Kingdom, Upper Volta, Uruguay, USA, USSR, Venezuela, W. Indies, and Yugoslavia.

SCIENTIFIC PROGRAM

The scientific program consisted of the Opening and Closing Plenary Sessions, the Congress Symposia, the Section Symposia and Panels, Contributed Papers, Informal Conferences, Workshops, Poster Sessions, and Film Presentations. With the exception of the Plenary Sessions and the Film Presentations, the Scientific Program was arranged into the following thirteen sections: (1) Systematics; (2) Genetics; (3) Physiology and Biochemistry; (4) Toxicology; (5) Ecology; (6) Behavior; (7) Social Insects and Apiculture; (8) Biological Control; (9) Medical and Veterinary Entomology; (10) Agricultural Entomology and Pest Management; (11) Forest Entomology; (12) Stored Products and Structural Insects; and (13) Pesticide Development, Management, and Regulation.

PLENARY SESSIONS

Opening Plenary Session

The Congress was called to order by President Curtis W. Sabrosky on Friday, August 20, at 10:30 a.m. in the International Ballroom of the Washington Hilton Hotel. The delegates were welcomed officially by Dr. R.J. McCracken, Associate Administrator, Agricultural Research Service, United States Department of Agriculture, and by Dr. Ray F. Smith, President of the Entomological Society of America. Afterwards, the Secretary General, Dr. George Anastos, made a series of announcements. The main speaker, Professor T.R.E. Southwood, addressed the Congress on the topic, "Entomology and Mankind."

Closing Plenary Session

The Closing Plenary Session was held on Friday, August 27, at 3:30 p.m. in the International Ballroom of the Washington Hilton Hotel. Professor Thomas R. Odhiambo addressed the Congress on the topic, "Entomology and the Problems of the Tropical World." Afterwards, the President of the Permanent Committee of the Congress, Dr. J.C.M. Carvalho, addressed the Congress and chaired the business meeting of the Congress. Dr. P. Freeman, Secretary of the Permanent Committee, presented the report of the Permanent Committee. Dr. D.F. Waterhouse spoke on behalf of the delegates and thanked the officers of the Congress and all of the Committees of the Congress. Dr. George Anastos made some closing announcements and said farewell to the delegates on behalf of the Secretariat of

the Congress. Dr. Curtis W. Sabrosky also bade farewell to the delegates and officially closed the Congress.

CONGRESS SYMPOSIA

The Congress Symposia, which are included in these Proceedings, were held during the mornings of five days, and a total of 15 symposia was presented. Because no other meetings were scheduled during these times, all of the Congress Symposia were well attended. The topics of the Symposia, the sponsoring section, and the dates of presentation were as follows:

SATURDAY, AUGUST 21

The diversity of insects and the dominance of the land (Section 1).

Natural factors affecting pest populations (Sections 10, 8, 5, and International Organization of Biological Control).

Pesticide Development (Sections 13 and 4).

MONDAY, AUGUST 23

Insects in extreme environments (Section 3).

Systems approach to pest management (Section 10).

Pesticide resistance I (Sections 13 and 4).

WEDNESDAY, AUGUST 25

Pheromones, allomones, and kairomones: their significance in insect biology (Section 6).

Modern achievements and innovations in biological control (Section 8).

The impact of the chlorofluorocarbons/ozone question on insecticidal aerosols (Section 13).

THURSDAY, AUGUST 26

Physiology and biochemistry of insect/host interactions (Sections 3, 5, and 8).

Changing patterns in the transmission of arthropod-borne disease (Section 9).

Tropical stored-product entomology (Section 12).

FRIDAY, AUGUST 27

Genetic control of insects (Section 2).

Communication and learning in social insects (Section 7).

Insect impacts on the quality of forest and urban environments (Section 11).

SECTION SYMPOSIA AND PANELS

A total of 92 symposia and panels was presented over a period of 7 days. Each of the 13 Sections of the Congress was involved in these presentations, and a number of Sections sponsored joint Symposia. The Symposia (number in parentheses) sponsored by each Section were as follows: Section 1 (12); Section 2 (4); Section 3 (5); Section 4 (7); Section 5 (6); Section 6 (6); Section 7 (6); Section 8 (9); Section 9 (4); Section 10 (10); Section 11 (4); Section 12 (5); and Section 13 (3). The Symposia (number in parentheses) sponsored jointly were as follows: Sections 3 and 2 (3); Sections 13 and 4 (2). Sections 3 and 7, 2 and 1, 1 and 5, 11 and 8, 13 and 12, and 11 and 12 sponsored one symposium each.

The topics, the sponsoring section, and the dates on which the symposia were held are as follows:

FRIDAY, AUGUST 20

The theory of classification (Section 1).

Hybrid sterility (Section 2).

Neuroendocrinology: homeostatic hormones (Section 3).
 Recent advances in insecticide metabolism (Section 4).
 Population quality (Section 5).
 Defensive behavior of insects (Section 6).
 Recent advances in ant and termite biology (Panel, Section 7).
 Recent advances in microbial control (Section 8).
 Sensory basis of behavior in blood-feeding insects (Section 9).
 Survey, detection, sampling, and economic thresholds in insect pest management (Section 10).
 Detection, evaluation, and prediction of forest pest insect populations (Section 11).
 Fumigants and their applications in stored-product entomology (Section 12).
 Pesticide residues and their relationship to pesticide management (Section 13).

SATURDAY, AUGUST 21

Endangered insects of the world (Section 1).
 Major directions in the future of the systematics of Hemiptera (Section 1).
 Neural circuitry for insect behavior (Section 3).
 Characterization and evaluation of insect colonies (Sections 3 and 2).
 Pesticides in aquatic environments (Section 4).
 Theoretical and practical assessment of predation in population dynamics of insects (Section 5).
 Recent advances in wasp and bee biology (Panel, Section 7).
 The role of hyperparasitism in biological control (Section 8).
 International programs to prevent pest spread (Section 10).
 Pest management in urban environments I (Section 10).
 Space and residual sprays in stored-product entomology (Section 12).
 Pesticide safety (Sections 13 and 4).
 International symposium on Carabidae I (Section 1).
 Pesticide degradation by aquatic organisms (Section 4).
 Standardization and safety of microbial pesticides (Section 8).
 Pest management in urban environments II (Section 10).

SUNDAY, AUGUST 22

Higher classification of Coleoptera (Section 1).
 Phase and caste determination: endocrine aspects (Sections 3 and 7).
 Insecticides for the future (Section 4).
 Reproductive competition, mate choice, and sexual selection in insects (Section 6).
 Foraging behavior in bees (Panel, Section 7).
 Biological control by augmentation of natural enemies (Section 8).
 Publicly supported control programs (Section 10).
 Assessment and prediction of pest insect impacts on forest uses and values (Section 11).
 Agricultural pests in international commerce (Section 13).

MONDAY, AUGUST 23

Application of genetics to insect systematics and analysis of species differences (Sections 2 and 1).
 Uses of tissue culture in physiology and biochemistry (Section 3).
 Insecticides as neurotoxins (Section 4).
 Evolution of escape in space and time I. (Section 5).
 Communicative behavior of insects (Section 6).
 Ant manipulation for biological control (Section 8).
 Systematics and biology of Ceratopogonidae I (Section 9).
 Host plant resistance: regional reports on research and development in resistance and economic usefulness of released crops (Section 10).
 Concepts and practice of integrated pest management in forestry (Section 11).

Infestation detection, sanitation, and loss assessments in stored-product entomology (Section 12).

Pesticide resistance II. (Sections 13 and 4).

Biosystematics of parasitic Hymenoptera (Section 1).

International symposium on Carabidae II (Section 1).

The higher classification of the orthopteroid insects (Section 1).

Developmental hormones, biosynthesis, binding, receptors, and metabolism (Panel, Section 3).

Evolution of escape in space and time II. (Section 5).

Production of microbial control agents (Section 8).

Systematics and biology of Ceratopogonidae II. (Section 9).

Host resistance in stored-product entomology (Section 12).

TUESDAY, AUGUST 24

Insecticide resistance III: biochemical genetics (Section 4).

WEDNESDAY, AUGUST 25

Continental drift and historical biogeography of insects (Section 1).

Induced sterility for insect control (Section 2).

Selected topics in insect embryology I (Sections 3 and 2).

Ecology and evolution of Anoplura and Mallophaga (Section 5).

Behavioral basis of insect-host plant interactions (Section 6).

Origin and evolution of nonreproductive castes in social insects (Panel, Section 7).

Pesticides and beneficial arthropods (Section 8).

Insect-borne disease problems associated with water and land resources development (Section 9).

Habitat modification for regulating pest populations (Section 10).

Pest management in protected culture crops (Section 10).

The role of application techniques in respect to safe and efficient pest control (Section 13).

International symposium on Carabidae III (Section 1).

Insects in stream ecosystems (Sections 1 and 5).

Recent advances in the study of scale insects (Section 1).

Effect of symbionts on insect reproduction (Section 2).

Toxicology of arthropod venoms (Section 4).

Orientation and foraging behavior in social insects (Panel, Section 7).

Pest management implementation — an international perspective (Section 10).

Novel approaches to forest insect control (Sections 11 and 8).

THURSDAY, AUGUST 26

Contributions of comparative morphology and embryology to arthropod phylogeny (Section 1).

Insect reproduction — spermatogenesis (Section 2).

Isozymes and their uses in entomological investigations (Sections 3 and 2).

Osmoregulation and active transport (Section 3).

Ecology of marine insects (Section 5).

Hormonal control of insect behavior (Section 6).

Social interactions among communal and primitively social Hymenoptera (Panel, Section 7).

Biological control of tansy ragwort (Section 8).

Uses of pesticides in integrated control programs (Section 10).

The role of arthropods in forest ecosystems (Section 11).

Insecticide resistance in stored-product insects (Section 12).

An international view of the significance and the control of urban pests (Sections 13 and 12).

FRIDAY, AUGUST 26

Orientation behavior of insects (Section 6).

Protozoa, nematodes, and fungi as microbial control agents (Section 8).

Insect pests of wood in structures (Sections 11 and 12).

INFORMAL CONFERENCES

A total of 26 Informal Conferences was held over a period of 7 days on a variety of topics. The number (in parentheses) which was sponsored by each Section was: Section 1 (4); Section 3 (7); Section 4 (1); Section 5 (4), Section 9 (1); Section 12 (7); and Section 13 (1). Sections 8 and 6 jointly sponsored one Informal Conference.

The topics, the sponsoring section, and the dates on which these Informal Conferences were held are as follows:

FRIDAY, AUGUST 20

Insect hemocytes and hemolymph (Section 3).

SATURDAY, AUGUST 21

The genus *Lygus* Hahn and its interactions with its host plants (Section 5).

Ecology of Tephritidae (Section 5).

Stored-product insect population ecology (Section 12).

Use of controlled and inert atmospheres in stored-product entomology (Section 12).

SUNDAY, AUGUST 22

Advances in microchemical analyses as applied to insect pheromones and hormones (Section 3).

MONDAY, AUGUST 23

Changing nature of entomological collections: uses, functions, growth, and management (Section 1).

UNESCO informal conference on global pesticide strategy (Section 13).

TUESDAY, AUGUST 24

Theoretical aspects of insect biogeography (Section 1).

Potential of remote sensing in the African tsetse program (Section 9).

Tabanid work conference (Section 1).

Behavioral and toxic actions of formamidine pesticides (Section 4).

Ecology of stem borers of maize (Section 5).

Aphididae: behavior, biology, ecology, and systematics (Section 5).

Pathogens of stored-product insects (Section 12).

Use of ionizing radiation in stored-product entomology (Section 12).

WEDNESDAY, AUGUST 25

Chemosterilization and insect control (Section 3).

Vertebrate resistance to arthropod parasites I (Section 3).

Kairomones and natural enemy behavior (Sections 8 and 6).

Selected topics in insect embryology II (Section 3).

Vertebrate resistance to arthropod parasites II (Section 3).

Stored-product acarology (Section 12).

Packaging and containerization (Section 12).

Stored-product insect pheromones and growth regulators (Section 12).

Diptera systematics, with special reference to family classification (Section 1).

THURSDAY, AUGUST 26

Steroid metabolism in insects (Section 3).

WORKSHOPS

Three workshops were held during the Congress. The topics, the sponsoring Section, and the dates on which these workshops were held are as follows:

SUNDAY, AUGUST 22

Electrophysiological techniques workshop (Section 3).

MONDAY, AUGUST 23

Recent advances in insect cytogenetic techniques (Section 2).

TUESDAY, AUGUST 24

Inheritance of susceptibility to infections in vectors (Section 2).

CONTRIBUTED PAPERS

A total of 456 contributed papers on a wide variety of subjects was presented over a period of 7 days. Also, 37 papers were read by title only during this same period. The presentation (in parentheses) according to Sections was: Section 1 (55); Section 2 (28); Section 3 (47); Section 4 (15); Section 5 (58); Section 6 (39); Section 7 (13); Section 8 (42); Section 9 (50); Section 10 (58); Section 11 (11); Section 12 (5); and Section 13 (18). A total of 5 and 12 papers was presented in joint sessions in Sections 5 and 9 and 11 and 8, respectively.

POSTER SESSIONS

Ten poster sessions on a variety of subjects were held on 5 days. A total of 95 titles was presented, and Sections 3, 4, 5, 6, 7, 8, 9, 10, 11, and 12 were represented. Four sessions were devoted to Section 3, whereas Sections 6 and 7 and 9, 11, and 12 were held jointly.

The poster sessions generated considerable interest and provided an excellent medium for discussing one's interests with others.

FILM PRESENTATIONS

A total of 45 films was shown over a period of 7 days. Of this total, 20 were shown twice and 5 were shown only once.

ASSOCIATED MEETINGS

Although they were not directly a part of the Congress, the following organizations or groups met in association with the Congress: Acarological Society of America (Informal Meeting); Coleopterists Society (1976 Annual Meeting); Eastern Branch of the Entomological Society of America (48th Annual Business Meeting); International Organization for Biological Control (I.O.B.C., 7th General Assembly); Commonwealth Institute of Biological Control (C.I.B.C., Staff Meeting); and Meeting of the Permanent Committee of the International Working Conferences in Stored-Product Entomology.

SOCIAL EVENTS

Three main social events were sponsored by the Congress for the entertainment and relaxation of the membership.

The first event was the President's Reception on Friday evening, August 20, in the beautiful International Ballroom of the Washington Hilton Hotel. Approximately 1900 members and guests of the Congress attended the President's Reception and were treated to cocktails, hors d'oeuvres, and music.

The second event was a special reception at the National Museum of Natural History, Smithsonian Institution, on Sunday evening, August 22. About 1800 members were in attendance and were provided with champagne and an opportunity to visit various Exhibit Halls of the Museum, including the newly opened Insect Zoo, featuring living insects in natural habitats.

The final social event was the Farewell Party which was held on Thursday, August 26, in the International Ballroom of the Washington Hilton Hotel. About 1350 members were in attendance and were treated to wine, cheese, and fruit as well as to music and an outstanding exhibition of ballroom dancing.

ASSOCIATES PROGRAM

A special program was organized for the Associate Members of the Congress. Highlights of the program were the four tours to points of interest in Washington, D.C. and nearby Virginia as well as the Hospitality Suite in the Washington Hilton Hotel.

The tours were well received and 50 Associate Members participated in each of the 4 tours for a total of 200. The Hospitality Suite was relatively well patronized and was a convenient place to meet each morning for complimentary coffee and pastry as well as for Associate Members to visit with each other.

TOURS

Of the 12 one-day excursions and the 13 longer excursions which were offered, all were eventually cancelled because of insufficient registration except 2 one-day excursions. These two were the Skyline Drive—Shenandoah Valley tour which had 89 participants and the Beltsville tour which had 112 participants.

EXHIBITS

Both commercial and noncommercial exhibits were displayed in the Exhibit Hall of the Washington Hilton Hotel from Friday, August 20, to Tuesday, August 24. Various chemical companies and other industries displayed a variety of products and equipment of interest to entomologists.

Noncommercial exhibits included an outstanding showing of entomological art. This art exhibit was organized by Elsie Froeschner and Elaine Hodges. Also featured among the noncommercial exhibits was a display of entomological research at the Beltsville Agricultural Research Center, U.S.D.A., and the book exhibit of the Entomological Society of America.

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SOCIETY

Entomological Society of America
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Richard M. Duffield	USA	Mrs. Morteza Esmaili	Iran
Howard T. Dulmage	USA	Romeo Estores	Philippines
Mrs. Howard T. Dulmage	USA	Paul Etkind	USA
Mary-Margaret Dulmage	USA	Mrs. Paul Etkind	USA
Brian J. Dumser	France	David L. Evans	USA
Robert W. Dunbar	Tanzania	Howard A. Evans	England
Curtis E. Dunn	USA	W. Bruce Ezell, Jr.	USA
Claude H. Dupuis	France	David Fabacher	USA
Mrs. Claude H. Dupuis	France	Homer E. Fairchild	USA
Lance A. Durden	USA	Mahlon L. Fairchild	USA
Samson R. Dutky	USA	Louis A. Falcon	USA
*N. Dutt	India	John H. Fales	USA
Zeliha Duzgunes	Turkey	Mrs. John H. Fales	USA
Victor A. Dyck	Philippines	Trevor Falloon	West Indies
Richard J. Dysart	USA	H. Fankhanel	E. Germany
Mrs. Richard J. Dysart	USA	Robert M. Faust	USA
Emmett R. Easton	Netherlands	Gerhard F. Fedde	USA
John L. Eaton	USA	Vicki H. Fedde	USA
Karen A. Eaton	USA	Brian A. Federici	USA
Walter Ebeling	USA	E.F. Feichtmeir	USA
Mrs. Walter Ebeling	USA	Dorothy J. Feir	USA

Lillian Feir.....	USA	Thomas Friedel	Canada
Gary M. Fellers	USA	William G. Friend.....	Canada
Joan Fellers.....	USA	Franco Frilli.....	Italy
*Giorgio A. Fenili.....	Italy	Ray Frisbie	USA
*Vincenzo Fenili.....	Italy	Max L. Frischnecht.....	Switzerland
*Mrs. Vincenzo Fenili.....	Italy	Austin M. Frishman	USA
Douglas C. Ferguson	USA	Richard C. Froeschner	USA
Mrs. Douglas C. Ferguson	USA	Mrs. Richard C. Froeschner	USA
Stephen Ferkovich.....	USA	Morton S. Fuchs.....	USA
Reeshon Feuer	USA	Erwin Fuehrer.....	Germany
Mrs. Reeshon Feuer	USA	Richard C. Funk.....	USA
Sandy B. Fiance	USA	David G. Furth	USA
William D. Field	USA	Njidda Gadzama	Nigeria
Thomas J. Fink	USA	C.C. Gagne	USA
Thelma Finlayson.....	Canada	James A. Gagne	USA
Jean R. Finney.....	Canada	Raymond J. Gagne.....	USA
Roland L. Fischer.....	USA	Robert Gair	England
D. Fish	USA	Mrs. Robert Gair	England
Ross E. Fishbough.....	USA	Andreas Gal	USA
Martha N. Fisher	USA	Rachel Galun	Israel
William F. Fisher	USA	Farduk M. Gamal-Eddin.....	Egypt
M. Fitz-Earle.....	Canada	George J. Gamboa	USA
Thomas R. Flanagan.....	USA	Ivan E. Gard	USA
R.F. Flattum	USA	G. Ronald Gardiner.....	England
Thomas H. Flavell	USA	Thomas P. Gargan	USA
G.A. Fleming	Colombia	Mrs. Thomas P. Gargan	USA
David J. Fletcher.....	South Africa	Lyn Garling	USA
Oliver S. Flint, Jr.	USA	C.F. Garner	USA
Mrs. Oliver S. Flint, Jr.	USA	Willa Garner.....	USA
Mary L. Flint	USA	Norman E. Gary.....	USA
Ralph Wills Flowers	USA	R. Gasser	Switzerland
Victor Fluck.....	Switzerland	Paul E. Gatterdam	USA
Richard H. Foote.....	USA	Timothy A. Gatzdner.....	USA
Laurine J. Ford	USA	Randy R. Gaugler.....	USA
G.G. Foster.....	Australia	Ian D. Gauld	England
George A. Foster.....	USA	Mrs. Ian D. Gauld	England
John E. Foster	USA	William A. Gebhart.....	USA
Mrs. John E. Foster	USA	Quinton A. Geering.....	England
William A. Foster	England	E.G. Gemrich II.....	USA
D.C. Fourie.....	South Africa	Adrian G. Gentile.....	USA
Mrs. D.C. Fourie.....	South Africa	Curtis Gentry.....	USA
H.W. Fowler.....	USA	Joseph W. Gentry	USA
Mrs. H.W. Fowler	USA	George P. Georghiou	USA
Lavros R. Fox	Australia	Eugene J. Gerberg	USA
*John G. Franclemont	USA	Charles F. Gerdes	USA
Andre Francoeur.....	Canada	Dan Gerling.....	Israel
Henry E. Frania	Canada	Eduard F. Gersabeck	USA
J. Howard Frank.....	USA	Mercury S. Ghilarov	USSR
G.W. Frankie	USA	Mrs. Mercury S. Ghilarov	USSR
J.M. Franz.....	Germany	Ahmad S.K. Ghouri	Pakistan
Mrs. J.M. Franz.....	Germany	Majori Giancarlo	Italy
James L. Frazier.....	USA	Areti-Marina Giannakakis.....	Australia
J.A. Freeman.....	England	David L. Gibo	USA
Jeffrey V. Freeman	USA	Marco Giglioli	West Indies
Paul Freeman.....	England	Lawrence Gilbert.....	USA
Mrs. Paul Freeman.....	England	Hagen R. Gillenwater	USA
Ashley H. Freiberg	USA	Cedric Gillott.....	Canada
Jerome E. Freier.....	USA	Mrs. Cedric Gillott.....	Canada
Jose A. Freire	USA	Matthew E. Gilson.....	USA
Richard Freitag.....	Canada	William F. Gimpel, Jr.	USA
*John French.....	Australia	Howard S. Ginsberg	USA
J. Freuler.....	Switzerland	William Ginsberg.....	USA
Paul H. Freytag.....	USA	Edward H. Glass	USA

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Aaron Goldberg	USA	Gordon E. Guyer	USA
Graham J. Goldsworthy	England	Robert W. Gwadz	USA
Lyle Goleman	USA	Hans Gysin	Switzerland
Victor I. Golini	Canada	Mrs. Hans Gysin	Switzerland
Florencio M. Gomez	Mexico	Vachik Hacopian	USA
Jugto G. Gonzalez	Philippines	Mahmoud Hafez	Egypt
Roberto H. Gonzalez	Italy	Mrs. Mahmoud Hafez	Egypt
Walter Goodman	USA	Henry Hagedorn	USA
*Carl Goodpasture	USA	Kenneth S. Hagen	USA
James T. Goodwin	USA	Mrs. Kenneth S. Hagen	USA
Gordon Gordh	USA	C.P. Haines	England
Fred M. Gordon	USA	Robert G. Haines	USA
R.D. Gordon	USA	Raziel Hakim	USA
Glenn A. Gorelick	USA	Gonzalo Halffter	Mexico
J.R. Gorham	USA	Mrs. Gonzalo Halffter	Mexico
William H. Gotwald, Jr.	USA	Jonathan P. Haliscak	USA
Mrs. William H. Gotwald, Jr.	USA	C.A. Hall	Australia
James L. Gould	USA	David G. Hall	USA
Henri Goulet	Canada	Michael J. Hall	USA
Albert E. Grable	USA	Robert D. Hall	USA
Zoran Gradojevic	Yugoslavia	Sharon Hall	USA
Charles L. Graham	USA	Edward Hallinan	USA
Jay E. Graham	USA	Edson J. Hambleton	USA
Owen H. Graham	USA	Dennis Hamel	USA
W.M. Graham	Canada	Abdul Hamid	Nigeria
Jeffrey Granett	USA	Mrs. Abdul Hamid	Nigeria
Marion Gratwick	England	Steven Wayne Hamilton	USA
R.C. Graves	USA	W.D. Hamilton	England
Thomas M. Gray	USA	S.M. Hammad	Egypt
James M.C.D. Grayson	USA	Philip J. Hamman	USA
D.O. Greenbank	Canada	Robert E. Hamman	USA
Les Greenberg	USA	Abner M. Hammond	USA
Sharon L. Greenberg	USA	P.M. Hammond	England
Albert Greene	USA	Steven N. Handel	USA
Kenneth W. Greenlee	USA	Elton J. Hansens	USA
E.C. Greiner	Canada	Frank E. Hanson	USA
*J. Linsley Gressitt	USA	George M. Happ	USA
Graham C.D. Griffiths	Canada	R. Haque	USA
J.L. Gringorten	Canada	J.M. Hardman	Australia
Edward E. Grissell	USA	D. Elmo Hardy	USA
Richard Groen	Canada	Mrs. D. Elmo Hardy	USA
William L. Grogan, Jr.	USA	Phillip K. Harein	USA
Paul Gross	USA	Mrs. Phillip K. Harein	USA
Arnoldus Cornelis Grosscurt	Netherlands	*Louie T. Hargett	USA
Marvin Grossman	Canada	Pierre P. Harper	Canada
Tom Gruenwald	USA	B. Jane Harrington	USA
Mary C. Gruetzmacher	USA	C. Leon Harris	USA
Leszek Grum	Poland	C.R. Harris	Canada
Madukar Guddewar	USA	E.J. Harris	USA
A.A. Guerra	USA	John W. Harris	Canada
Delfa Guiglia	Italy	Peter Harris	Canada
E. Gunthart	Switzerland	Mrs. Peter Harris	Canada
Mrs. E. Gunthart	Switzerland	Bruce A. Harrison	USA
A.P. Gupta	USA	Larry Hart	USA
Ashley B. Gurney	USA	W. Keith Hartberg	USA
Panduro Gustano	Bolivia	James S. Harvey	USA
W.D. Guthrie	USA	Sirajul Hasan	France
Andrew P. Gutierrez	USA	Mrs. Sirajul Hasan	France
Jorge Gutierrez	Mexico	Caryl P. Haskins	USA
Laura Gutierrez	Mexico	Mrs. Caryl P. Haskins	USA
Jorge Gutierrez Jr.	Mexico	S.A. Hassan	W. Germany
Mrs. Jorge Gutierrez	Mexico	M.P. Hassell	England

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Richard Hayes.....	USA	Robert M. Hollingworth.....	USA
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Kirby L. Hays.....	USA	Robert G. Holmberg.....	Canada
*Mark E. Headings.....	USA	Preben Holst.....	Denmark
J. Heath.....	England	Gerald G. Holt.....	USA
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Karl-Johan Hedquist.....	Sweden	Harry Hoogstraal.....	USA
Mrs. Karl-Johan Hedquist.....	Sweden	T.H. Hoppe.....	Switzerland
Abraham Hefetz.....	USA	Freda Horay.....	USA
Herman J. Heikkinen.....	USA	Ernst Horber.....	USA
Arthur M. Heimpel.....	USA	David J. Horn.....	USA
Bernard Heinrich.....	USA	Klaus Horstmann.....	Germany
Ernst Heiss.....	Austria	Robert W. Hoskins.....	USA
Mrs. Ernst Heiss.....	Austria	Mohamed M. Hosny.....	Egypt
R.G. Helgesen.....	USA	Dennis F. Howard.....	USA
Klaus Hellenbrand.....	Canada	Francis G. Howarth.....	USA
Bruce S. Heming.....	Canada	H.F. Howden.....	Canada
Lyman S. Henderson.....	USA	Mrs. H.F. Howden.....	Canada
Charles S. Henry.....	USA	C.T. Howe.....	England
J.E. Henry.....	USA	R.W. Howe.....	England
Thomas J. Henry.....	USA	G.M. Howse.....	Canada
John B. Heppner.....	USA	James B. Hoy.....	USA
Lee H. Herman, Jr.....	USA	Marjorie A. Hoy.....	USA
Henry Hermann.....	USA	Stephen A. Hoying.....	USA
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R.A. Herrett.....	USA	Chao-Yen Hsieh.....	USA
Jon L. Herring.....	USA	Tai-Fang Hsueh.....	USA
Gerard D. Hertel.....	USA	Yiau-Min Huang.....	USA
Gary F. Hevel.....	USA	Michael D. Hubbard.....	USA
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*Berndt Heydemann.....	W. Germany	Ralph E. Hubner.....	USA
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Mrs. Norman E. Hickin.....	England	Milton Davis Huettel.....	USA
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Mrs. Toshitaka Hidaka.....	Japan	Idwal Wyn Hughes.....	Bermuda
Friedrich Hieke.....	Germany	Mrs. Idwal Wyn Hughes.....	Bermuda
Henry A. Highland.....	USA	J. Huignard.....	France
Clarence H. Hill.....	USA	Mrs. J. Huignard.....	France
Dennis S. Hill.....	Hong Kong	Joe H. Hultquist.....	USA
Donald F.J. Hilton.....	Canada	Hans E. Hummel.....	USA
Chester M. Himel.....	USA	Pieter J. Hummelen.....	Indonesia
Howard E. Hinton.....	England	James H. Hunt.....	USA
Edward T. Hitchen.....	England	Linda-Margaret Hunt.....	USA
Judith M. Hitchen.....	England	Lucien Huot.....	Canada
Ronald W. Hodges.....	USA	Mrs. Lucien Huot.....	Canada
Mrs. Ronald W. Hodges.....	USA	Paul D. Hurd, Jr.....	USA
Ernest Hodgson.....	USA	Mrs. Paul D. Hurd, Jr.....	USA
Clifford E. Hoelscher.....	USA	William S. Hurt.....	USA
Thomas Hofacker.....	USA	D. Hutson.....	England
Buzz L. Hoffmann.....	USA	George Hutton.....	USA
Clarence H. Hoffman.....	USA	Mrs. George Hutton.....	USA
Mrs. Clarence H. Hoffman.....	USA	Phil Hutton.....	USA
Hellmut Hoffmann.....	Germany	Mrs. Phil Hutton.....	USA
Jules A. Hoffman.....	France	K.E. Hyland.....	USA
Harold C. Hofman.....	USA	O.L. Idowu.....	Nigeria
David B. Hogg.....	USA	*Kazuo Ikeda.....	USA

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Mrs. Toshiaki Ikeshoji	Japan	Jerome Jones	USA
T.J. Imholte	USA	Michael D.R. Jones	England
Zehra Imran	India	Rhondda E. Jones	USA
Mary Jo Ingram	USA	Richard L. Jones	USA
David W. Inouye	USA	Robert H. Jones	USA
May N. Inscoe	USA	Jan C. Jonkman	USA
Yiannakis M. Ioannou	USA	Anthony M. Jordan	England
Rosemary J. Irving-Bell	W. Australia	William H. Jordan, Jr.	USA
Michael E. Irwin	USA	Jag Mohan Joshi	USA
Dennis L. Isaacson	USA	Erich Jost	Germany
Mrs. Dennis L. Isaacson	USA	Mirko Jovanic	Yugoslavia
Isaac Ishaaya	Israel	R.J. Joyce	England
J. Ishay	Israel	Mrs. R.J. Joyce	England
Shoziro Ishii	Japan	Gerald L. Jubb	USA
Conrad Istock	USA	Charles L. Judson	USA
Yosiaki Ito	Japan	Mrs. Charles L. Judson	USA
*J.L. Ivey	USA	Kenneth Judy	USA
Edward E. Ivy	USA	Mrs. Kenneth Judy	USA
Mrs. Edward E. Ivy	USA	Abul K.M.F. Kabir	Bangladesh
Syun'Iti Iwao	Japan	Walter J. Kaczor	USA
Kisabu Iyatomi	Japan	*Sampurno Kadarsan	Indonesia
Arata Izeki	Japan	Heinrich Kaiser	Germany
Louis Jackai	USA	Margarete Kalin	Canada
Robert D. Jackson	USA	Karim Kamali	Iran
Martin Jacobson	USA	M.P. Kambysellis	USA
Richard L. Jacques, Jr.	USA	Ann E. Kammar	USA
Albert Jaeger	Germany	Mervyn A. Kamran	USA
Pierre Jaisson	France	Mrs. Mervyn A. Kamran	USA
Margaret James	USA	Keiji Kanamitsu	Japan
Surachate Jamornmarn	USA	Alan I. Kaplan	USA
Rudolf Jander	USA	Inder P. Kapoor	USA
H. Janetschek	Austria	Jalil S. Karam	USA
Antti Jansson	Finland	A.H. Kaschef	Egypt
Daniel H. Janzen	USA	Georgann L. Kates	USA
Iraj Javadi	USA	W.R. Kaufman	Switzerland
M. Javahery	Iran	David H. Kavanaugh	USA
Mrs. M. Javahery	Iran	Susumu Kawabe	USA
Edward G. Jay	USA	Harry K. Kaya	USA
Mrs. Edward G. Jay	USA	Clyde W. Kearns	England
Robert L. Jeanne	USA	Larry L. Keeley	USA
C.A.W. Jeekel	Netherlands	M. Kehat	Israel
Mrs. C.A.W. Jeekel	Netherlands	J. Keiding	Denmark
Donna H. Jez	Canada	Clifford B. Keil	USA
Eleazar J. Jimenez	Mexico	James E. Keirans	USA
Roberto Johansen	Mexico	William R. Kellen	USA
Clarence D. Johnson	USA	Brian L. Kelley	USA
Donald R. Johnson	USA	Thomas J. Kelly	USA
Mrs. Donald R. Johnson	USA	Eugene E. Kenaga	USA
Donn T. Johnson	USA	Peter E. Kenmore	USA
Eric L. Johnson	USA	George Kennedy	USA
Franklin M. Johnson	USA	John S. Kennedy	England
Mrs. Franklin M. Johnson	USA	Patty A. Kessler	USA
Laura K. Johnson	USA	D. Keith Kevan	Canada
Michael D. Johnson	USA	Abd E.F. Khalifa	Egypt
Mrs. Michael D. Johnson	USA	G. Khalil	USA
Paul C. Johnson	USA	Mohamed A.Q. Khan	USA
Victor Johnson	USA	A. Khushigian	USA
Warren T. Johnson	USA	Ke Chung Kim	USA
Mrs. Warren T. Johnson	USA	David S. King	USA
Pierre H. Jolivet	France	Robert C. King	USA
Davy Jones	USA	John M. Kingsolver	USA
*Hugh I. Jones	Australia	D.N. Kinn	USA

Keizi Kiritani	Japan	Daniel Robert Kucera.....	USA
Lawrence R. Kirkendall.....	USA	John E. Kuenberg	USA
Edwin W. Kisiedu	Ghana	Nancy T. Kuenzel.....	USA
Ryoiti Kisimoto	Japan	Jehoshua Kugler	Israel
Kiniti Kitayama	USA	A.P. Kulkarni	USA
James B. Kitzmiller	USA	H.M. Kulman.....	USA
Jeff Klahn	USA	R. Kumar.....	Ghana
Waldemar Klassen.....	USA	*Virendra Kumar	West Indies
George E. Klee	USA	Janice E. Kuster	Canada
William H. Klein	USA	F.W. Kutz	USA
W.J. Kloft	Germany	Robert Kwietniak	USA
H. Klomp.....	Netherlands	Renato M. Labadan	Philippines
Hein Louis Klopping	USA	Wallace E. LaBerge	USA
J.A. Klun	USA	Leo LaChance	USA
Fred W. Knapp	USA	Rene D. Lafont	France
Virgil R. Knapp	USA	Marshall Laird	Canada
Janice G. Knausenberger.....	USA	Hsiao-Ling Lam	USA
Walter I. Knausenberger	USA	K.P. Lamb	New Guinea
Edward F. Knipling.....	USA	Mrs. K.P. Lamb	New Guinea
Mrs. Edward F. Knipling.....	USA	Richard Y. Lamb.....	USA
Henry M. Knizeski, Jr.	USA	*Neil J. Lamb	USA
Charles O. Knowles	USA	M. Lambert.....	USA
Herbert Knutson	USA	Gerolf Lampel	Switzerland
Lloyd V. Knutson.....	USA	Emmett P. Lampert.....	USA
Mrs. Lloyd V. Knutson.....	USA	Vladimir Landa	Czechoslovakia
*Je-Ho Ko.....	Korea	G.N. Lanier	USA
R.W. Kobylnyk.....	Canada	Beatrice Lanzrein.....	Switzerland
Henry G. Koch	USA	James H. Lashomb.....	USA
J.P. Kochansky	USA	Mohamed A. Latheef.....	USA
Carlton S. Koehler	USA	John Lattin.....	USA
John K. Koeppe.....	USA	David Lauer	USA
H.K. Koerner	Germany	G. Lauge.....	France
Marcos Kogan.....	USA	Arthur G. Lavallee	Iran
Stephen N. Kogge.....	USA	*Michael P. Lavalleye	USA
L.T. Kok.....	USA	John F. Lawrence	USA
Mrs. L.T. Kok.....	USA	Ralph Scott Lawrence	USA
Douglas M. Kolodny	USA	Fred A. Lawson	USA
Konstantin N. Komblas	Greece	John H. Lawton.....	England
Nels M. Konnerup	USA	Arden O. Lea	USA
Dennis D. Kopp	USA	Scott A. Leach.....	USA
Nicholas A. Kormilev	USA	Mary G. Leahy	USA
Michael Kosztarab.....	USA	Homer M. LeBaron.....	USA
Clemens Kotter	Germany	Valentin A. Lebedev	USSR
Costas A. Kouskolekas.....	USA	Philippe Lebrun.....	Belgium
Juro Koyama	Japan	*Farida Lebthahi.....	Algeria
Sandra K. Kraft.....	USA	George Leonard LeCato	USA
Jay H. Krall	USA	B. Lamar Lee	USA
James P. Kramer	USA	Mrs. B. Lamar Lee	USA
*Karl J. Kramer	USA	*Kyung Ro Lee	Korea
Michel Kremer	France	Robert Lee	Canada
R.I. Krieger	USA	Wen-Yung Lee	Taiwan
Frank L. Kriger	Canada	James G. Leesch	USA
Jan Krikken.....	Netherlands	Thomas F. Leigh.....	USA
James B. Kring	USA	Mrs. Thomas F. Leigh.....	USA
William L. Krinsky	USA	A.M. Leloup	Belgium
Mrs. William L. Krinsky	USA	Georges Le Masne	France
Niels P. Kristensen.....	Denmark	M. Lenz.....	Germany
Gene Kritsky	USA	Gladys Leon.....	Nicaragua
Mrs. Gene Kritsky	USA	David E. Leonard	USA
Karl V. Krombein.....	USA	Roger A. Leopold.....	USA
James L. Krysan.....	USA	Norman C. Leppla	USA
Yukio Kubota	USA	Eugene Lessard	USA
Mrs. Yakio Kubota.....	USA	R. Leuthold.....	Switzerland

Clement Levac	Canada
Mrs. Clement Levac	Canada
Marshall D. Levin	USA
Richard Levy	USA
Franklin B. Lewis	USA
Trevor Lewis	England
W. Joe Lewis	USA
Jenifer M. Lichtenfels	USA
Mark Licker	USA
James Liebherr	USA
Guan Soon Lim	Malaysia
*Guan-Tick Lim	W. Malaysia
Orlando Lindo	Nicaragua
Mrs. Orlando Lindo	Nicaragua
Donald Lindquist	USA
Mrs. Donald Lindquist	USA
Carl H. Lindroth	Sweden
R.L. Linkfield	USA
John R. Linley	USA
E. Gorton Linsley	USA
Mrs. E. Gorton Linsley	USA
Jack E. Lipes	USA
Mrs. Jack E. Lipes	USA
Dick R.L. Lipsey	USA
James A. Litsinger	Philippines
Marcia Litte	USA
Robert J. Little, Jr.	USA
James E. Lloyd	USA
Grace Lo	USA
Michael Locke	Canada
Richard A. Lockshin	USA
Donald J. Lococo	Canada
Karen E. Loeblich	USA
Werner J. Loher	USA
James B. Lok	USA
Mrs. James B. Lok	USA
Astrid Löken	Norway
Lucrecio Lara Londono	Colombia
J.F. Longworth	New Zealand
Hugo de Souza Lopes	Brazil
Mrs. Hugo de Souza Loipes	Brazil
Nancy Lorimer	USA
Svata M. Louda	USA
Spiro J. Louloudes	USA
Mosco Love	USA
J. Byron Lovell	USA
Alan D. Lowe	New Zealand
Yael Lubin	Canal Zone
Esther Lubzens	USA
Robert F. Luck	USA
William H. Luckmann	USA
Mrs. William H. Luckmann	USA
H.W. Ludwig	Germany
M.J. Lukefahr	USA
Albert E. Lund	USA
Mrs. Albert E. Lund	USA
Denise G. Lundry	USA
Martin Lüscher	Switzerland
Mrs. Martin Lüscher	Switzerland
Peter Luthy	Switzerland
Robert L. Lyon	USA
William W. Macdonald	England
Mrs. William W. Macdonald	England
Raul V. MacGregor-Loaeza	Mexico
Manfred Mackauer	Canada
D.S. MacLachlan	Canada
David R. Maddison	Canada
P.A. Maddison	England
S.H.P. Maddrell	England
Gunter W.H. Madel	W. Germany
Chuka L. Madubunyi	Nigeria
Edwin D. Magallona	Philippines
Ivanka T. Maglic	USA
J. Marshall Magner	USA
Mrs. J. Marshall Magner	USA
Joseph Mahar	USA
Gay D. Maher	USA
Ali A. Mahmoud	USA
Chris T. Maier	USA
Klaus Maksymov	Switzerland
Stanley E. Malcolm	USA
Hans Malicky	Austria
Arnold Mallis	USA
*Baldev S. Mangat	USA
Jerome V. Mankins	Honduras
*Gary V. Manley	USA
A.V. Manouchehri	Iran
Nabil A. Mansour	USA
M.A. Manzelli	USA
Mrs. M.A. Manzelli	USA
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Jose A. Mari Mutt	USA
Hubert Markl	Germany
E.N. Marks	Australia
Edwin P. Marks	USA
Carlos Marquez-Mayaudon	Mexico
Mrs. Carlos Marquez	Mexico
Paul M. Marsh	USA
Warren K. Marshall	Canada
Mrs. Warren K. Marshall	Canada
William Marshall	USA
Ethelbert C. Martin	USA
Edward A. Martinko	USA
Sinzo Masaki	Japan
L. Masner	Canada
Peter Masner	Switzerland
Thomas L. Mason, Jr.	USA
Ed C. Masteller	USA
Babajide Matanmi	Nigeria
Irene Matejko	USA
M.E. Materu	Tanzania
Wayne N. Mathis	USA
Gustave Mathys	France
R. Matsuda	Canada
F. Matsumura	USA
Patricia C. Matteson	USA
*John Matthew	South Africa
G.A. Matthews	England
H.B. Matthews	USA
Robert W. Matthews	USA
Willy Matthey	Switzerland
*Mrs. Willy Matthey	Switzerland
William J. Mattson	USA
Fowden G. Maxwell	USA
H.M. Mazzone	USA
Samuel R. Mbise	USA

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Stuart G. McCausland.....	USA
R.J. McClanahan	Canada
George A.H. McClelland.....	USA
E.S. McCluskey	USA
David McComb.....	USA
Elzie McCord, Jr.....	USA
Earl D. McCoy	USA
*A.W.R. McCrae.....	England
Ian C. McDonald.....	USA
Peter B. McEvoy.....	USA
F.L. McEwen.....	Canada
William H. McGaughey	USA
T.P. McGovern.....	USA
E.R. McGovran	USA
David G. McHaffey	USA
Susan B. McIver.....	Canada
R.J. McKenna	USA
Donald L. McLean	USA
John A. McLean.....	Canada
J.M. McLeod	Canada
Michael L. McManus	USA
Jeremy N. McNeil	Canada
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Alston B. Meade	USA
W. Meier.....	Switzerland
Venezia Melamed-Madjar	Israel
*Luis Mellado.....	Spain
*Mrs. Luis Mellado.....	Spain
Jean J. Menier	France
Arnold S. Menke	USA
Mrs. Arnold S. Menke	USA
J.J. Menn	USA
Robert E. Menzer	USA
Edward P. Merkel.....	USA
Richard W. Merritt.....	USA
Carlos Mery	USA
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C.D. Michener.....	USA
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S.J. Miles	England
Mrs. S.J. Miles	England
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Douglass R. Miller.....	USA
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Jeffrey C. Miller.....	USA
Richard W. Miller.....	USA
Scott E. Miller.....	USA
Tom A. Miller	USA
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Hayk Mirzayans.....	Iran
Mrs. Hayk Mirzayans.....	Iran
Teruyuki Misumi.....	Japan
B.K. Mitchell	Canada
Carl J. Mitchell.....	USA
Robert T. Mitchell.....	USA
Takashi Mitsui	USA
Edward L. Mockford.....	USA
A.K.A. Mohamed.....	USA
Mrs. A.K.A. Mohamed.....	USA
Mohamed Mohamedsaid	USA
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William A. Molesworth	England
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Judith A. Mollet.....	USA
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Ulric Mondesir	Canada
H. Montagner	France
*G.G. Montgomery	Canal Zone
Rick Moody	Canada
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Chester G. Moore	Puerto Rico
Mrs. Chester G. Moore	Puerto Rico
Norman Moore.....	England
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*O. Morales	USA
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V.C. Moran.....	South Africa
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Anne Morgan.....	Canada
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Neal O. Morgan.....	USA
Philip B. Morgan.....	USA
Hans Mori.....	Japan
Rokuya Morimoto	Japan
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Oswald N. Morris.....	Canada
P.E. Morrison.....	Canada
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Vintcent Mortons.....	USA
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Lawrence Mound	England
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Gonzalo E. Moya Borja.....	Brazil
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Abdulrahman S. Msangi	Tanzania
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Mir S. Mulla	USA
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Leonard E. Munstermann.....	USA
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*Carol A. Musgrave	USA
*M. Muthu	India
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Judith H. Myers	Canada
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Sueo Nakahara	USA
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Toshio Nakashima	Japan
S.S. Nakat	USA
William Nakayama	USA
Toshio Narahashi	USA
Sudhir Narang	Brazil
J.S. Naresh	USA
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John Wm. Neal	USA
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Howard D. Nelson	USA
Judd Nelson	USA
Robert H. Nelson	USA
Mrs. Robert H. Nelson	USA
W.A. Nelson	Canada
Mrs. W.A. Nelson	Canada
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Mrs. Harald Nemenz	Austria
H.H. Nesbitt	Canada
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Jos. Wm. Newbold	Scotland
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Mrs. D.G. Nielsen	USA
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P.C. Nigam	Canada
Fred Nijhout	USA
Mary Nijhout	USA
Chamneam Nilprapai	USA
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Masaru Nishikawa	Japan
Chikao Nishino	USA
Jay Nixon	USA
G. Nogge	Germany
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Mrs. Charles H. Noirot	France
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Mrs. Guido Nonveiller	Yugoslavia
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Uzi Nur	USA
Kenneth E. Nuss	USA
Ifedioramma E. Nwana	Nigeria
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Jack O'Brien	USA
Barry M. O'Connor	USA
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L.E. O'Keeffe	USA
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Gerald Odland	USA
Adelani Ogunrinade	Nigeria
Michio Ohba	Japan
Eiji Ohnishi	Japan
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Tetsuya Ohtaki	Japan
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Nemanja Ostojic	Yugoslavia
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Ruth B. Otitoju	Nigeria
Eiji Otsuka	Japan
Christian Otto	Norway
James L. Overman	USA
Daniel Overstreet	USA
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James S. Packer	USA
Rajindar Pal	India
*Pachagounder Palaniswamy	Canada
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Mrs. William A. Palmer	Australia
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Mary C. Papageoriou	USA
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Larry G. Pappas	USA
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Bruce L. Parker	USA
Douglas Parker	USA
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Dale W. Parrish	USA
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Stewart B. Peck.....	Canada	Ron Prokopy	USA
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Jorge E. Pena.....	Colombia	Mrs. Hubert Pschorn-Walcher	Switzerland
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Mrs. J. Phipps	Canada	Niphan C. Ratanaworabnan.....	Thailand
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Grahame E. Pratt.....	England	Arthur Retnakaran.....	Canada
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Stuart Reynolds.....	USA	Mrs. Curtis W. Sabrosky.....	USA
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*Mrs. A. Glenn Richards.....	USA	Mrs. Reece I. Sailer.....	USA
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Mrs. Richard L. Ridgway.....	USA	Mrs. Seiroku Sakai.....	Japan
Robert E. Ridsdale.....	USA	Syo Sakurai.....	Japan
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Karla S. Ritter.....	USA	K. Sander.....	Germany
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A. Sterett Robertson.....	USA	Roger E. Sandquist.....	USA
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Mrs. A. Grant Robinson.....	Canada	Jamilton P. Santos.....	USA
Dennis W. Robinson.....	USA	Mrs. Jamilton P. Santos.....	USA
William H. Robinson.....	USA	T. Sasaba.....	Japan
George C. Rock.....	USA	Miss Takako Sasakawa.....	Japan
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George R. Roemhild.....	USA	Mrs. Mitsuhiro Sasakawa.....	Japan
Jean-Claude Roger.....	USA	*Remesh Chandra Satija.....	India
G.G. Rohwer.....	USA	Masataka Sato.....	Japan
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Mary H. Ross.....	USA	Harry M. Savage.....	USA
C.J. Rossetto.....	Brazil	R.M. Sawicki.....	England
Philippe A. Rossignol.....	Canada	Alan J. Sawyer.....	USA
Ann E. Rotariu.....	USA	Kailash N. Sazena.....	India
T.F. Roth.....	USA	S.C. Saxena.....	India
Eric Rothenbuhler.....	USA	John E. Scanlon.....	USA
Hilda Rothenbuhler.....	USA	Mrs. J.E. Scanlon.....	USA
Walter C. Rothenbuhler.....	USA	George A. Schaeffers.....	USA
Mrs. Walter C. Rothenbuhler.....	USA	Glen W. Schaeffer.....	England
Adrien J. Roudier.....	France	Joseph C. Schaffner.....	USA
Mrs. Adrien J. Roudier.....	France	James M. Schalk.....	USA
Subrata Roy.....	India	Michael E. Schauff.....	USA
J.G. Rozen.....	USA	Donald J. Schliessmann.....	USA
Mrs. J.G. Rozen.....	USA	Evert I. Schlinger.....	USA
Nguyen Ru.....	USA	*Mrs. Evert I. Schlinger.....	USA
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Kurt Russ.....	Austria	Fred H. Schmidt.....	USA
Helen E. Russell.....	USA	Gerald T. Schmidt.....	USA
Louise M. Russell.....	USA	Günter Schmidt.....	W. Germany
Mercer P. Russell.....	USA	Justin O. Schmidt.....	USA
John M. Ruth.....	USA	Lea Schmidt.....	Yugoslavia
Donald A. Rutz.....	USA	Edward T. Schmidtman.....	USA
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Michael F. Ryan.....	Ireland	R. Schonbrod.....	USA
Roger B. Ryan.....	USA	D.A. Schooley.....	USA

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Kennet R. Schrankel	USA	H.P. Shurtleff	USA
F. Schremmer	W. Germany	*John Shuttleworth	Australia
Robert F.W. Schroder	USA	H.R. Shuyler	Italy
M.E. Schroeder	USA	Mrs. H.R. Shuyler	Italy
P.M. Schroeder	USA	Ciril Sidor	Yugoslavia
William J. Schroeder	USA	Juan A. Sifuentes	Mexico
Randall T. Schuh	USA	Rizo Sijaric	Yugoslavia
Seymour Schulman	USA	James M. Silverman	USA
G.G.M. Schulten	Netherlands	Robert M. Silverstein	USA
George K. Schumaker	USA	John B. Simeone	USA
Michael F. Schuster	USA	Mrs. John B. Simeone	USA
Fritz Schwalm	USA	Joseph Simkin	USA
Paul H. Schwartz, Jr.	USA	Hal G. Simkover	USA
Meyer Schwarz	USA	Mrs. Hal G. Simkover	USA
Donald Schwert	Canada	Donald E. Simonet	USA
Nigel E. Scopes	England	Samuel Singer	USA
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J. Mark Scriber	USA	R.N. Sinha	Canada
Geoffrey G. Scudder	Canada	Sunthorn Sirivanakarn	USA
William D. Seabrook	Canada	Norman Sladen	Belgium
Robert J. Searle	England	James A. Slater	USA
Burkhard J. Sechser	Switzerland	Mr. James A. Slater	USA
James R. Sedell	USA	Elbert L. Sleeper	USA
Bonnie J. Sedlak	USA	Eleanor H. Slifer	USA
F. Sehnal	Czechoslovakia	Mitchell Slobodnik	USA
*Larry G. Sellers	USA	Robert L. Smiley	USA
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Hanna Seryczynska	Poland	E. Laidlaw Smith	USA
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Lin Shanahan	Australia	Mrs. Ray F. Smith	USA
D.L. Shankland	USA	Thomas Smyth, Jr.	USA
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Ted J. Shapas	USA	Edwin L. Soderstrom	USA
Martin Shapiro	USA	M. Soehardjan	Indonesia
M.L. Sharma	Canada	Achmad T. Soemawinata	USA
Mrs. M.L. Sharma	Canada	Sardar S. Sohi	Canada
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*Dale Sharp	USA	A. Sokoloff	USA
S.S. Sharp	USA	Christer Solbreck	Sweden
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J. Shejbal	Italy	Mrs. John O. Solem	Norway
*Yun-Ping Josephine Shen	Taiwan	A.A. Soliman	Egypt
Julian Shepherd	USA	Saad Soliman	Egypt
Martin Sherman	USA	Helen Sollers-Riedel	USA
Ralph W. Sherman	USA	J.D. Solomon	USA
Guy Shewell	Canada	Michael G. Solomon	England
David B. Shibles	USA	S.B. Soloway	USA
T.R. Shieh	USA	Ali Akbar Soltani	Iran
Michael Shinkle	USA	Mrs. Ali Akbar Soltani	Iran
Harry H. Shorey	USA	Daniel E. Sonenshine	USA
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Andrew Spielman.....	USA
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James Steffel	USA
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Warren Steiner	USA
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Bruce A. Steinly.....	USA
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Chr. Stenseth	Norway
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Vernon M. Stern	USA
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Edmund Stevenson	USA
J. Rees Stevenson	USA
James A. Stewart.....	USA
R.K. Stewart	Canada
George C. Steyskal	USA
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Lavina Stuart	USA
Tuyosi Sugimoto	Japan
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William Sullivan.....	USA
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Shozo Takahashi	Japan
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Y. Tanada.....	USA
Manabu Tanaka	Japan
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Lionel R. Taylor.....	England
R.A.J. Taylor	England
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Donna Tegelman	USA
William H. Telfer	USA
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Paul H. Terry	USA
Henry A. Terwedow, Jr.....	USA
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H.A. Thomas	USA
John G. Thomas	USA
John H. Thomas.....	USA
F. Christian Thompson.....	USA
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Malcolm J. Thompson.....	USA	Mrs. R. van den Bosch	USA
Raymond G. Thompson.....	USA	Dale O. Van Denburg.....	USA
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H.P. Tipnis.....	India	Mrs. J. van der Vecht.....	Netherlands
Wolfgang O. Tischler.....	W. Germany	H.F. Van Emden.....	England
S.S. Tobe	Canada	J. C. van Lenteren	Netherlands
A.H. Tomerlin.....	USA	Mario A. Vaughan.....	Pakistan
Torolf R. Torgersen	USA	James L. Vaughn.....	USA
James G. Touhey.....	USA	H.H.W. Velthuis.....	Netherlands
Michael Kaney Tourtellot.....	USA	George L. Venable.....	USA
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Mrs. Henry K. Townes	USA	Maria Verdu.....	USA
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John E. Treherne	England	Amador Villacorta.....	Brazil
Ray Treichler.....	USA	David Vincent.....	USA
E. Tremblay.....	Italy	Sandra Vincent.....	USA
Mrs. E. Tremblay.....	Italy	S. Bradleigh Vinson	USA
R.K. Tripathi.....	USA	Mrs. S. Bradleigh Vinson	USA
Mrs. R.K. Tripathi.....	USA	Paul H. Visscher	USA
Robert L. Trivers.....	USA	Saralee N. Visscher.....	USA
Milan Trpis.....	USA	Ford A. Vogel	USA
James W. Truman.....	USA	Gregory N. Vogel.....	USA
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Richard Trumbull.....	USA	Walter Vogel	Switzerland
James H. Tsai.....	USA	Hans D. Volkart.....	Switzerland
Ching H. Tsao.....	USA	Hasso Kurt von Eickstedt	Mexico
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George Tsiropoulos.....	Greece	J.R. Voshell.....	USA
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John R.G. Turner	USA	Dale E. Wagoner.....	USA
David C. Twinn	England	Mrs. Dale E. Wagoner.....	USA
*M.E. Tzanakakis.....	Greece	Barbara M. Waite	USA
Matazaemon Uchida.....	Japan	Nobel Wakabayashi	USA
E. Uebel	USA	Yoshio Waku	Japan
Shun-Ichi Ueno.....	Japan	G.P. Waldbauer	USA
Norihiro Ueshima.....	Japan	Harry G. Walker	USA
Staffan Ulfstrand	Sweden	Mrs. Harry G. Walker	USA
Hans Ulrich.....	Germany	Thomas J. Walker.....	USA
Kasumbogo Untung	USA	William F. Walker	USA
William M. Upholt.....	USA	J. Bruce Wallace.....	USA
Mrs. William M. Upholt.....	USA	Gordon D. Waller.....	USA
Rafael Urrelo.....	USA	William E. Wallner	USA
*Efana J. Usua	Nigeria	Naoejda Waloff	England
*Mrs. E.J. Usua	Nigeria	F. Walsh.....	Upper Volta
Joyce A. Utmar.....	USA	Michael C. Walters.....	South Africa
Luis Valencia	USA	Cheryl C. Walton	USA
Barry D. Valentine.....	USA	Thomas Walton	USA
Karl R. Valley	USA	*Kurt Walzhofer.....	Austria
C. van Achterberg	Netherlands	Anthony J. Wapshere.....	France
Lucas Van Balen	USA	Mrs. Anthony J. Wapshere.....	France
Robert C. Vandehey.....	USA	*Richard B. Ward	USA
Gerrit van de Klashorst.....	USA	Richard D. Ward	Brazil
John D. Vandenberg.....	USA	Robert D. Ward	USA

Ronald A. Ward	USA
Edmund G. Warner	USA
Monica Warshaw	USA
Douglas F. Waterhouse	Australia
Mrs. Douglas F. Waterhouse	Australia
William E. Waters	USA
Doreen Watler	Canada
Alan K. Watson	Canada
Allan Watson	England
Mrs. Allan Watson	England
David L. Watson	USA
*J.A.L. Watson	Australia
*Frederick Watters	Canada
William T. Waugh	USA
Michael Way	England
Joseph E. Weaver	USA
A.J.S. Weaving	Rhodesia
Mrs. A.J.S. Weaving	Rhodesia
David P. Webb	USA
Donald W. Webb	USA
Ralph E. Webb	USA
James A. Webster	USA
Howard V. Weems, Jr.	USA
R. Wehner	Switzerland
Mathis H. Weiden	USA
Donald E. Weidhaas	USA
Jeffrey A. Weier	USA
Medeea Weinberg	Romania
Gunter F. Weirich	USA
Jaroslav Weiser	Czechoslovakia
Donald M. Weisman	USA
Mrs. Donald M. Weisman	USA
Mitchell J. Weiss	USA
*Christian F. Weisser	USA
*Stephen M. Welch	USA
William G. Wellington	Canada
Stanley G. Wellso	USA
Rupert L. Wenzel	USA
Richard A. Werner	USA
Ronald M. Weseloh	USA
Stephen Wesley	USA
Mary Jane West-Eberhard	Colombia
Richard L. Westcott	USA
Peter Weygoldt	Germany
*Mark E. Whalon	USA
Bob Wharton	USA
G.A. Wheatley	England
Marshall R. Wheeler	USA
Mrs. Marshall R. Wheeler	USA
Ronald E. Wheeler	USA
Alfred G. Wheeler, Jr.	USA
Arthur A. Whipp	USA
Robert F. Whitcomb	USA
Willard H. Whitcomb	USA
Mrs. Willard H. Whitcomb	USA
Michael J. White	Australia
Richard E. White	USA
Donald R. Whitehead	USA
Joseph T. Whitlaw, Jr.	Canal Zone
Richard J. Whitman	Canada
Mrs. Richard J. Whitman	Canada
W. Keith Whitney	USA
Mrs. W. Keith Whitney	USA
Frederick W. Whittemore	USA
Gullermo J. Wibmer	USA
W. Wichard	Germany
Frederico M. Wiendl	Brazil
*Mrs. Frederico M. Wiendl	Brazil
Glenn B. Wiggins	Canada
Mrs. Glenn B. Wiggins	Canada
Sir Vincent Wigglesworth	England
C. Wiklund	Sweden
Christopher Wilkinson	England
Jack D. Wilkinson	USA
Rowland N. Wilkinson	USA
Carroll M. Williams	USA
L.M. Williams	USA
Michael L. Williams	USA
Robert Williams	England
Harold R. Willson	USA
*Edward O. Wilson	USA
Shannon W. Wilson	USA
Thomas G. Wilson	USA
John A. Winder	Brazil
Patrick S. Wingo	USA
R.G. Winks	Australia
Willis W. Wirth	USA
Mrs. Willis W. Wirth	USA
Walter Wirtz	Germany
John A. Witter	USA
Mrs. John A. Witter	USA
Lloyd A. Witting	USA
Walter Wittmer	Switzerland
Daniel P. Wojcik	USA
Mrs. Daniel P. Wojcik	USA
John D. Wollam	USA
Catherine R. Wood	USA
David L. Wood	USA
Mrs. David L. Wood	USA
Donald Wood	Canada
Francis E. Wood	USA
Frederic E. Wood	USA
Jonathan C. Wood	USA
R.J. Wood	England
Mrs. R.J. Wood	England
Stephen L. Wood	USA
Robert E. Woodruff	USA
Alison Woodworth	USA
R.J. Wootton	England
R.B. Workman	USA
James E. Wright	USA
Valerie Wright	USA
Donald P. Wright, Jr.	USA
William H. Wymer	USA
Rene Wyniger	Switzerland
M. Wysoki	Israel
Mariann Wyss-Huber	Switzerland
Shigemi Yagi	Japan
I. Yamamoto	Japan
Kageyuki Yamaoka	Japan
Keiko Yamashita	Japan
Tosiro Yasuda	Japan
Keizo Yasumatsu	Japan
Harry O. Yates III	USA
Wesley Eugene Yates	USA
Shoshana Yathom	Israel

David F. Yen.....Taiwan
Lee Fong-Chen YenTaiwan
William G. Yendol.....USA
Scott R. Yocom.....USA
Wayne A. YoderUSA
Masayoshi YoshidaJapan
Toshiharu Yoshida.....Japan
Carl M. YoshimotoCanada
Chen-Wen YoungUSA
David A. Young.....USA
Mrs. David A. Young.....USA
G. Young.....New Guinea
Lester C. Young.....USA
Orrey P. Young.....USA
Peter E. YoungUSA
William R. YoungThailand
Mrs. William R. YoungThailand
Ching G. YuUSA

Takeshi Yushima.....Japan
Al-Yafi Zafer.....USA
Dmytro Zajciw.....Brazil
*Lauren Green Zarate.....USA
Nasser ZarehUSA
Thomas J. Zavortink.....USA
Brian ZeichnerUSA
Ingeborg Zenner-PolaniaColombia
J.L. ZettlerUSA
E. ZielkeLiberia
Mrs. E. ZielkeLiberia
E. ZlotkinIsrael
G.W. Zoebelin.....W. Germany
Oscar C. ZoebischUSA
Eliezer Zomer.....USA
Robert Zwart.....Netherlands
Gunter ZweigUSA
Peter Zwick.....W. Germany

*Registered but not in attendance



Permanent Committee for the International Congresses of Entomology. *Seated*, left to right: Mound (Secretary Elect), Freeman (Secretary), Carvalho (Chairman), Ghilarov (Vice Chairman), Baccetti. *Standing*, left to right: Smith, Lindroth, Tischler, Yasumatsu, Waterhouse, Sabrosky, Pal, Landa, Hafez. Absent: Taylor.



Stage party at the opening session: The Permanent Committee (see above), plus Secretary-General Anastos (back row, left end), Dr. T. A. Taylor (back row, 3rd from left), Dr. H. J. McCracken (front row, 3rd from left; official welcome), and Dr. T. R. E. Southwood (front row, 4th from left; opening plenary speaker). The vacant chair is that of President Sabrosky, who was presiding at the podium.



President Curtis W. Sabrosky



Secretary-General George Anastos



T. R. E. Southwood, opening plenary speaker



Thomas R. Odhiambo, closing plenary speaker

Opening Plenary Session

(Led by President Sabrosky, the members of the Permanent Committee and Drs. McCracken and Anastos marched to their places on the platform. The meeting was opened with the national anthem, "The Star Spangled Banner," played by the Special Ceremonial Unit of the Navy Band, conducted by Chief Musician Art Accardo. The President thanked them for the music provided during the assembling period.)

Members of the Congress, Distinguished Guests, Ladies and Gentlemen:

For a formal welcome from this country, from our federal government, and from Washington, I introduce to you Dr. Ralph McCracken, Associate Administrator of the Agricultural Research Service of the U.S. Department of Agriculture. Dr. McCracken.

(Dr. McCracken)

Thank you, Dr. McCracken, for your words of welcome for this Congress.

The initiative for inviting the XV Congress to this country came from the Entomological Society of America. To represent the entomologists of the host country, I introduce to you Dr. Ray F. Smith, of the University of California at Berkeley, President of the Entomological Society of America. President Smith.

(Dr. Smith)

Thank you, President Smith, for your welcome from the Society and from American entomologists.

At this time, I wish to call upon Dr. George Anastos, Secretary-General of the Congress, for a few announcements that need to be made at this time. Dr. Anastos.

(Dr. Anastos)

Thank you, Mr. Secretary-General.

Introductions

(1) The Congresses of Entomology have a very few Honorary Members. Four are living, and one is here today. I am honored to introduce the distinguished insect physiologist from Cambridge University, England, Sir Vincent Wigglesworth.

(2) The Honorary Vice Presidents of the Congress are the president of the Entomological Society of America, and the presidents of the entomological societies of our good neighbors to the north and south — Canada and Mexico. The president of the Entomological Society of America has already been introduced. I am honored to present to you the President of the Entomological Society of Canada, Dr. George Cooper, and the President of the Sociedad Mexicana de Entomología, Dr. Jorge Gutierrez Samperio.

(3) The last previous entomological Congress in this country was held at Cornell University, Ithaca, New York, in 1928, nearly a half century ago, and the president of the Congress was one of America's world famous entomologists, Dr. L.O. Howard. I am pleased to introduce a member of that Congress and Dr. Howard's devoted companion, his daughter, Miss Lucy Howard. There are a few other members of this XV Congress who were also members of that IV Congress in 1928. Would those members stand and be acknowledged by the Congress? (The President recognized Louise Russell, Alan Stone, Floyd Smith, Dwight DeLong, Edson Hambleton, Frank Campbell, Mrs. R.E. Snodgrass.) We thank you for your enduring and steadfast interest in entomology and in the Congresses.

(4) I am sure that all Congresses would like to be innovative. I propose to make this Congress unique in at least one way: introduction of the Permanent Committee for International Congresses of Entomology. At the XIV Congress in Canberra, in 1972, my wife reported to me that someone near her asked "Who are all those people up there on the platform?" And I realized that although the Permanent Committee is always seated in a prominent place at the opening meeting, the members have never, in my memory, been introduced to a Congress. Therefore, may I introduce them now. Will each rise and be recognized as I call his name? Please — no applause for each individual; wait until

all are introduced and then we can applaud the Committee as a whole. (President Sabrosky introduced individually the members of the Permanent Committee.)

And now that I have given them their moment in the limelight, I propose to kick them off the stage. Will the Permanent Committee and Dr. McCracken and Dr. Anastos please move quickly to their reserved seats in the audience?

As they leave the platform, I may note that Dr. Waterhouse was President of the XIV Congress in Canberra in 1972; Dr. Ghilarov was Secretary-General of the XIII Congress in Moscow in 1968; and Dr. Freeman was Secretary-General of the XII Congress in London in 1964. So we can feel the hot breath of history as these gentlemen view the proceedings of this Congress.

It is not my intention to make a formal presidential address, but I do wish to make a few remarks at this time.

The International Congresses of Entomology have had a long and distinguished history. The first Congress was held in Brussels in 1910, and was attended by 250 members from 23 countries. The membership fee for that first Congress was the princely sum of 25 Belgian francs, or about \$5.00 at that time. Times have changed! That first Congress was so successful and enjoyable that another was arranged only two years later, at Oxford, England, in 1912. After a long gap during and after World War I, Congresses resumed with a 3-year interval; since 1956, a 4-year interval. The largest Congress was that at Moscow in 1968, with over 2,900 in attendance, and the second largest that at London in 1964, with over 1,800. Our Congress, in spite of the difficulties of inflation, austerity, budget problems, etc., in many parts of the world, will now be the second largest, with over 2,000 registered.

The 15 Congresses have been held in 13 different countries. England has hosted two Congresses, and this is our second. If I may be pardoned a personal item, this is my 8th Congress of Entomology, so I have attended over half of the 15 Entomology Congresses. My experience began with the VII Congress at Berlin in 1938, an experience that lives in pleasant memory. I would like very much to reminisce with memories of my seven previous Congresses, but time and demands of the XV Congress dictate otherwise.

No Congress has ever been perfect, and it is safe to say that none ever will be. I know that we have made some mistakes, despite good intentions and sincere efforts. We apologize humbly for these, and we beg your indulgence and your tolerance. Planning Congresses is difficult at best. Perhaps a Congress held in good times with a healthy world economy would not be subject to as many worries as we have had. However, even in the best of times, Congress planners need cooperation. I know that we have irritated some people by stringent requirements for pre-registration, dollar payments, housing, etc. But perhaps our experience and our methods will assist future Congresses in deciding what to do — perhaps what not to do.

The scientific program provides more time for symposia than for individual papers. It has long been recognized that the plethora of individual papers is one of the worst features of Congresses. At least one Congress in another field eliminated contributed papers altogether. This step seemed too drastic a break with the past for an entomological congress, but as an intermediate step we have emphasized carefully organized programs. Each morning is devoted to three major symposia, or a total of 15, one from each of the 13 Congress sections plus two others. For afternoons, sectional symposia and invited speakers are given major attention. We believe in this way a strong, solid program has been arranged.

We have tried a few so-called poster sessions, a recently developed means of handling a large number of contributed papers. Undoubtedly this is a new method for many of you. We hope that you will give this method a good try, or at least be interested in having the experience, for future reference.

I know that many entomologists are interested in postage stamps. We tried very hard to get a special insect stamp for the Congress but without success, chiefly because of the emphasis on historical subjects in this Bicentennial year of 1976. However, we believe that our efforts helped direct attention to the beauty and interest of insect stamps, and we understand that work is now going on for a set of 4 butterfly stamps to be issued in 1977.

Dr. Anastos has mentioned the President's Reception, and for the benefit of late comers, this is now scheduled for 7:00-9:00 o'clock this evening. Please be advised that you are not required to pass through a receiving line and shake my hand. You may do so, if you wish, *provided* that you do not hold my hand too long nor squeeze it too hard.

We hope that you enjoy our beautiful capital city of Washington. This is the Bicentennial Year for this country — our 200th anniversary as a nation. We are as a mere child compared with the

nations from which many of you come, but we are nevertheless proud of our 200 years of democracy. There are many special events and special exhibits in the city in connection with the Bicentennial. We hope that you find time to sample some of these and to visit our outstanding historical, cultural, and educational features.

Finally, for the Americans present, remember that this Congress is not hosted only by the officers of the Congress, or the Organizing Committee. Each of us is one of the hosts. May we all do our best to help make this a most memorable and pleasurable Congress for our fellow entomologists and their families from across the oceans and from other countries in the Western Hemisphere.

Our speaker at this opening plenary session is Professor T.R.E. Southwood, head of the Department of Zoology and Applied Entomology of the Imperial College of Science and Technology in London, England. His early work dealt with the taxonomy, morphology and biology of Hemiptera-Heteroptera and culminated in a large book, on the "Land and Water Bugs of the British Isles" by Southwood and Leston (1959). In the course of his biological work, he studied the immature stages, flight activity, mechanism of wing polymorphism, and insect-host relationships. So it was a natural move into studies of insect populations, sampling methods, etc., and he has become known in the last decade or so as an insect ecologist. I would cite particularly his 1966 book on "Ecological Methods with particular reference to the study of insect populations" and his editorship of the symposium on "Insect Abundance" (1968), a symposium of the Royal Entomological Society of London.

I am honored to introduce to you Professor Southwood, who will address you on the subject of "Entomology and Mankind."

Final Plenary Session

President Sabrosky: This is the final plenary session of the XV International Congress of Entomology. The speaker on this occasion is Professor Thomas R. Odhiambo, Professor at the University of Nairobi in Kenya, and Director of the ICIPE, the International Centre for Insect Physiology and Ecology, in Nairobi. Professor Odhiambo will address you on the subject "Entomology and the Problems of the Tropical World." Professor Odhiambo.

(Professor Odhiambo)

(President Sabrosky turned the meeting over to Chairman Carvalho of the Permanent Committee for the Congresses.)

President Sabrosky: Ladies and Gentlemen: We approach the final moments of the XV Congress. Will all those who helped with the Congress stand and be acknowledged? (Applause). We hope that you have enjoyed the Congress and have profited from the many meetings and the opportunities for personal contacts with friends old and new. There have been some sad happenings during the Congress. Our sympathies to families, friends, and colleagues. But life must go on, and does go on. Some of us will meet again, others will not. But for now, the officers and the entire staff of the XV Congress wish you all a safe trip home, and happy and productive days ahead in entomology. Thank you, and farewell!

Secretary-General Anastos has a few final announcements.

RESOLUTION AND ANNOUNCEMENTS SUBMITTED BY THE PERMANENT COMMITTEE

1. *Resolution from Section 1 on Scientific Collecting, Exchange and Transfer of Entomological Specimens*

WHEREAS, entomological specimens are indispensable material for the educational and scientific study of insects and other arthropods, and;

WHEREAS, entomological collections are permanent scientific resources, which are held in trust for use by the world scientific community, and;

WHEREAS, scientific collecting, exchange and transfer of entomological specimens is necessary in order to continue scientific inquiry and its rational application for the well-being of mankind, and;

WHEREAS, it is important that national and state regulations do not impede the appropriate use of scientific specimens in entomological research and education, and;

WHEREAS, the principle should be strongly endorsed that, where suitable museums exist for the safe long-term preservation of holotypes, these holotypes should be located in the region of the world where the species concerned occur, now

THEREFORE BE IT RESOLVED, that the XVth International Congress of Entomology, Washington, D.C., August 19-27, 1976 endorses the principle of exchange of scientific specimens of insects and other arthropods among scientists of all nations, and urges that when national and state regulations are made they be drawn in such a way that they are consistent with the foregoing preamble.

2. *Location of Next Congress*

An invitation to hold the next International Congress in Japan in 1980 was received from Dr. S. Masaki, President of the Entomological Society of Japan. The Committee recommended that this be accepted.

3. *Changes in the Composition of the Permanent Committee*

Dr. P. Freeman had expressed his wish to resign after 12 years of secretaryship and the Committee regretfully accepted his resignation. Resignations have also been received from Dr. G. Richard and Dr. C.H. Lindroth.

The Committee has been fortunate in being able to nominate Dr. L.A. Mound (United Kingdom) to replace Dr. Freeman both on the Committee and as Secretary.

The Committee also proposed that the following be appointed members of the Permanent Committee: —

Dr. E. Biliotti	(France)
Dr. S. Glumac	(Yugoslavia)
Dr. M. Hafez	(Egypt)
Dr. J. Keiding	(Denmark)
Dr. C.E. Machado-Allison	(Venezuela)

4. *Honorary Members of Congress*

The deaths were reported with regret of Professor J. Chester-Bradley and Dr. K. Holdhaus. It was proposed that Dr. C.H. Lindroth, a retiring Committee Member be appointed a new Honorary Member.

The foregoing resolution, recommendations and proposals, submitted by the Permanent Committee were approved by the Plenary Session of Congress.

IN REMEMBRANCE

POWERS S. MESSENGER.—It is with regret that we announce the death of Professor Powers S. Messenger, Chairman of the Department of Entomological Sciences, University of California, Berkeley, on Monday, August 16, 1976, in Berkeley. Born in Redding, California, August 14, 1920, Professor Messenger received both his Bachelor of Science Degree (1942) and his Ph.D. degree in Agricultural Chemistry (1951) at the University of California, Berkeley, and joined the University as an entomologist in 1951. In 1965 he was appointed professor of entomology. He was Chairman of the Department since 1973. His research included the influences of temperature on growth and reproduction of insects, the ecology and biological control of the Oriental fruit fly and the relationships between various other pest insect and parasite systems. Contributions in Dr. Messenger's memory may be made to the Powers S. Messenger Memorial Fund in care of the Department of Entomological Sciences, University of California, Berkeley 94720.

FATHER WALTER W. KEMPF, OFM.—Father Kempf, recently appointed Professor at the Department of Animal Biology, University of Brasilia, editor of the Brazilian

magazine *Studia Entomologica*, died suddenly of a massive coronary attack Friday, 20th August, at 2 AM at the Providence Hospital, after receiving all possible care from his Franciscan Order Brothers.

His body was sent to Brazil — Sao Paulo — according to the arrangement made between the two Provincial superiors.

He brought a paper to be presented at the Congress, "A Preliminary Zoogeographical Analysis of a Regional Ant Fauna in Latin America," and was finishing the memorial issue of the *Studia Entomologica* in honor of Father Thomas Borgmeier, the former editor, who died last year.

Entomology and Mankind

T.R.E. SOUTHWOOD

Department of Zoology & Applied Entomology, Imperial College, London

Entomology is a science that has some of its origins in both theology and art. Even today there is an aspect that might be said, from the skills demanded, to be an art and other facets that can fairly claim a place in the fine arts. The breadth of the subject contributes to its fascination. It is a hobby and also a profession; indeed for some it can be both without in any way restricting their intellectual experience. This plurality in the genesis of entomology may be seen in the dictionary definitions; whilst the Oxford and other British dictionaries generally describe it as 'that part of natural history that treats of insects,' French and American dictionaries tend to define it as a 'branch of zoology.' It is perhaps surprising that in 1745 the Swiss entomologist Charles Bonnet entitled his book "Traité d'insectologie" and expressed the view that "entomology" had a barbarous sound.

The many facets of entomology mean that it has impinged on mankind in multiple ways. There is firstly that corpus of science and art that strictly constitutes entomology and many persons have derived pleasure from it, just as they may from literature, art, or some useless but intellectually demanding branch of learning, heraldry or chess. The objects of this study, the insects, do however affect mankind as a whole: through both health and food supply. In many fields insects are man's greatest competitors and therefore though our subject is intellectually satisfying in its own right, it has to many, if not all of us, the added, perhaps overriding satisfaction of contributing to the alleviation of human suffering and the better management of the biosphere. The challenge of our subject is now greater and broader than ever. Having the great privilege of reviewing it before this Congress I intend to examine each of these aspects in turn: pleasure, welfare, and the management of the biosphere, co-existence.

Entomology's role in culture and recreation

In ancient Egypt the scarab beetle (*Scarabaeus sacer* L.) had an important place in religion and writing. The ball of dung it forms and rolls to provide an oviposition site was considered to represent the sun. Hence the scarab hieroglyph, pronounced 'Khopi' or 'Kleper,' represented the verb "to create" or "to become" and scarab images, both large and small, were widespread. The small seal images, that often had messages underneath such as 'Ammon protecteth' or 'Mut give thee long life', were particularly common in the New Kingdom (1580-1150 BC). The honey bee and fly were also represented by hieroglyphs (Harpaz 1973), but unlike the scarab these remained word pictures and did not become a phonetic symbol. There is a handsome representation of an aculeate, probably a bee, on the funerary bed of Queen Hetephras. Honey bees were widely depicted in the ancient world; this was generally associated with the function of providing honey and wax and will be discussed later.

Insects have also had an important role in lore and culture in other parts of the World, and I can only briefly allude to a few examples. The Praying Mantis has the major place in bushman mythology: the fact that the male dies during copulation (eaten by the female) emphasizes the cycle of death and rebirth, central to so many religions (van der Post 1961). Butterfly migrations involving at least 28 species (Williams 1958) are conspicuous in Sri Lanka and it was considered that these were pilgrimages to the sacred mountain, which is therefore called Samanala Kanda (Butterfly mountain). The honey bee has generally been extolled in lore, but with characteristic realism towards sexual

activities, in Indian literature it is compared with a lover, sipping nectar and moving on to a new loved one; in contrast the moth at a candle is like a lover who, unable to establish contact with his beloved (the candle) dies. Insects were sufficiently part of every day life in the sixth century BC for them to figure in Aesop's fables, whilst in the Mycenaean era the mythological Psyche was sometimes portrayed as a butterfly (Morge 1973).

Entomology, as we know it, had its slender beginnings in the writings of Aristotle, although the works of Chung Pzu show that the ancient Chinese philosophers also had some concept of metamorphosis (Needham 1956). After the collapse of the Roman Empire it was not until the Renaissance that entomology, like many other fields of human endeavour, again advanced. Initially the early encyclopaedic naturalists like Aldrovandi were as much scholars as observers and much reliance was placed on the works of classical authors: for example, Philemon Holland (1601) translated Pliny the Younger. However, Pliny and the medieval compilers had a strongly anthropocentric view of the Insecta, almost all the species discussed were those that impinged on health or food production, but the butterfly and firefly were included.

The first books entirely devoted to entomology were Aldrovandi's (1602) 'De Animalibus Insectis' and the multiple authored 'Theatrum Insectorum,' which contains contributions by Gesner, Wotton, Penny and was completed by Thomas Mouffet in about 1598. It was published in Latin in 1634 and an english translation in 1658. In the next hundred and fifty years the study of entomology made striking advances and publications ranged from Swammerdam's (1669, 1737) magnificent anatomical studies through Réamur's (1734-42) six volume memories to Moses Harris (1766) 'Aurelian' (Beier 1973, Tuxen 1973). Swammerdam and other invertebrate anatomists, such as Redi and Malpighi established the concept that insects were organized creatures with internal systems and life-cycles. Réamur emphasized the role of direct observation. The publication of Moses Harris' book may be taken to mark the formal development in England of entomology as a pastime. 'The Aurelian' gives a finely illustrated account of butterflies and moths and how to collect them. Originally published as a series of parts, each with a fine hand-coloured plate usually dedicated to a member of the nobility, its text was in English and French and it passed through several editions (Lisney 1960).

In the eighteenth century persons interested in entomology came together to form entomological societies, indeed perhaps the first in the World was the 'Aurelian Society' that existed in London in 1743, if not earlier: its books and collections, housed at the Swan Tavern, Exchange (now Change) Alley, perished in the great fire of Cornhill of 1748: the fire started in a nearby wigmaker's and the members narrowly escaped the same fate! The term 'Aurelia' had been used, since 1607, for the chrysalis of a butterfly. A succession of societies developed in Britain over the next hundred years, some were entitled 'Aurelian', others 'Entomological' (Neave 1933, Ford 1945). The Entomological Club, founded in 1826, still exists and is the oldest entomological organization in the World. Its membership has always been limited to 8 persons and its function is principally social. Its main impact nowadays is in the organization of the 'Verrall Supper' for entomologists held annually in London since 1912: it also 'spawned' the South London, now the British, Entomological and Natural History Society (James 1973).

On 31st January 1832 the Société Entomologique de France was founded and a year later, in March 1833, the (Royal) Entomological Society of London. These are now the oldest scientific societies and the great majority of the members of the latter are professional entomologists, but at the time of their foundation the professional entomologist hardly existed. It is interesting to examine the early membership of these Societies: of the 156 members in the first ten years of the Entomological Society of London, no less than eleven were noblemen, headed by a duke; there were only nine professionals — interpreting that concept widely enough to include Charles Darwin. A study of the membership list in *Bull.Soc.Ent.France* Vol. 1 shows a similar picture. Other national entomological societies were formed in Europe, towards the end of the nineteenth century. In 1906 national entomological societies were formed in Egypt and the USA; the former containing a majority of non-professionals, particularly lawyers. The Entomological Society of Ontario (= Entomological Society of Canada) started the publication of a national journal, the 'Canadian Entomologist' in 1868, five years after its foundation (Bethune 1868).

Very broadly the persons who established and joined these national societies had their primary concern in entomology in one of three main ways: as a pastime, as a branch of zoology or as the scientific basis for pest control. As I stressed before these are not mutually exclusive, but it is interesting to compare the strengths of the different components in various countries. A comparison

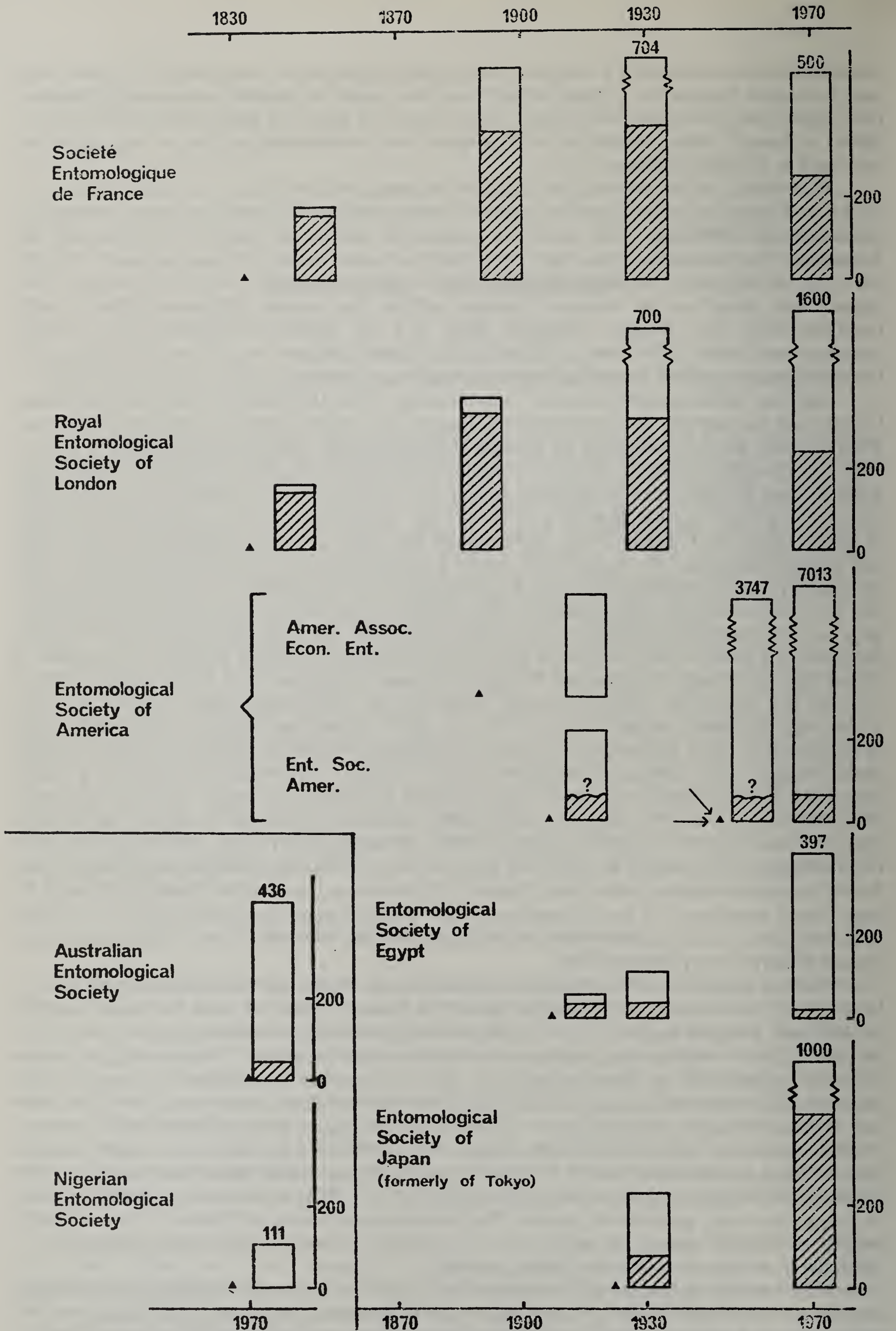


Fig. 1. —The growth and composition of the membership of various national entomological societies. (Shaded portion represent members for whom entomology is not their livelihood; triangles mark date of foundation).

of the amateur (= pastime) component in the membership of some national entomological societies is shown in Fig. 1. Three facts emerge:

- (i) Significant numbers of amateur entomologists are found in national societies only in Western Europe and Japan.
- (ii) Although the proportion of amateur entomologists in the European Societies may have fallen during this century, especially in the Royal Entomological Society of London, the actual numbers have not decreased significantly.
- (iii) In Japan both the proportion and actual numbers of amateurs seems to have increased.

I will speculate later on the causes of the early development of entomology as a pastime in Western and Central Europe and in Japan. In most parts of the industrial world many local entomological societies were founded in the middle part of the nineteenth century. In London for example there were several 'working mens' societies, often meeting in public houses.* In 1862 the "East London Entomological Society" met regularly at the "Bell & Mackerel." Of these only the "South London," now renamed the 'British Entomological and Natural History Society' still survives and a review at the time of its foundation remarked that it did not meet at a public house and "we believe the social position of the members is higher — but the working-man element is represented" (James 1975). During the Victorian era in Britain entomological exhibitions were regularly held, widely advertised and commented upon in the national press (Stanley-Smith 1953), whilst entomologists and insects often figured in cartoons.

In North America, likewise, some local societies were started (Sabrosky 1956, Gurney 1976) e.g., the Brooklyn in 1872 with 5 founders. The members of these societies, described as "wielders of the butterfly net or beetle bottle," were often clergy or teachers (Bethune 1868). Undoubtedly the collection of beautiful objects is a common practice in industrial countries becoming extended to all sections of society when their leisure time and housing conditions for storage, permitted this. However, as a writer in the (London) *Standard* newspaper of 19 October 1888 said "Entomology [is] of such scientific importance. In the days before Darwin a moth was simply a moth — one more addition to the corked drawers of the cabinet, another name added to the ever lengthening lists — But since the strange discoveries that led to Darwin's theory a Naturalist no longer values a 'specimen' simply as a 'specimen', but as a link between two others already known —. The important observations regarding mimicking among insects form an apt illustration of this." Thus the collectors pastime became transformed into the scientific study. Then, as now, the collection of insects frequently commenced in childhood, but once started the attractions of bionomic or physiological studies are realized (e.g., Wigglesworth 1965). The value of insects for science was comprehensively reviewed at the last Congress by E.H. Smith (1973).

Although, probably because of urbanization, entomology has not perhaps kept its comparative position amongst leisure activities in this century, it still flourishes. In Japan, as Dr. S. Iwao informs me, there are "many local entomological associations"; in North America there are specialized societies for Lepidoptera and Coleoptera and in Britain the predominantly non-professional British (formerly 'South London') Society has doubled its membership since the last War (James 1975). A measure of the general interest retained in, for example, butterflies in Western Europe may be gauged from the success of Higgins & Riley's 'A Field Guide to the Butterflies of Britain & Europe' (1970) which has appeared in eight languages and sold over 65,000 copies.

Economic entomology, the third component, first played a major role in one of the two parent bodies of our host society: the American Association of Economic Entomologists which was founded in 1889. For a long time this was the only entomological society whose founders and members were primarily concerned with the economic impact of insects on man. For the other nineteenth century societies this was a secondary interest, although as early as 1834 the (Royal) Entomological Society of London advised the sugar-cane growers of Grenada on the control of *Saccharosydne saccharivora* (Westwood). However, most societies founded in the last two decades, e.g., the Nigerian Entomological Society, have been more like the A.A.E.E. in approach: in the Proceedings of the first and second conferences of the Nigerian Society the emphasis is clearly placed on the applied aspects (*Proc. ent. Soc. Nigeria* vol. 1). The world-wide recognition of the value of entomologists to mankind has led to the growth of the entomological profession, the majority of whose members, I hope, enjoy

*'Public house' is a British term for houses that sell alcoholic drinks, i.e., taverns, beer cellars, bars.

their work and might in another century have been amateurs. The attendances at these International Congresses (Fig. 2) is some measure of the growth of our profession.

I would now like to consider briefly the early development of entomology as a pastime in Western and Central Europe and Japan, compared with the rest of the World. The principal factors involved seem to be:

- (1) The existence of an 'aristocracy' and a substantial professional middle class that had leisure and sought both to collect beautiful objects and to acquire knowledge.
- (2) Religious attitudes to nature and the taking life.
- (3) The ease of preserving collections.

The Société Entomologique de France was founded under the Presidency of M. Luczot, Chief Engineer for Bridges and Roads; Entomological Society of London under Mr. J.G. Children, the son of a banker, and the Librarian of Antiquities at the British Museum. These professional men, lawyers, doctors, engineers, bankers and, especially, clergymen, were soon joined by members of the nobility (as already mentioned these constituted nearly 10% of the membership). The importance of their role was not so much in their actual contribution to entomology, but in setting a general trend in collecting beautiful objects and accumulating knowledge. It is noteworthy that Moses Harris dedicated most of his plates to a member of the aristocracy. In the Netherlands in the same period, illustrations of European and South American Lepidoptera were being made and published by Maria Merian, Countess of Nuremburg. As we have seen other socio-economic groups would follow this lead, but although insects were (and are) auctioned, with skill, hard work and an element of luck, the poor clerk could obtain a better specimen than a duke. In Japan the same influences seem to have existed but for longer periods. From the 11th-12th centuries there is the story of Mushi Mezuru Himegimi (The Lady who Loved Insects), a princess who collected and reared insects (Konishi & Ito 1973), and today the Japanese Imperial family is active in zoological work.

Following St. Augustine, the western Christian could be further encouraged in his entomological work by regarding it as an act of piety. Both the title page and the frontispiece of the Aurelian have quotations from the Psalms (104 v. 24 & 111 v. 2). A different attitude prevailed in the Indian sub-continent: under the influence of the Buddhist and Hindu religions all life was revered. The cycle of reincarnation, as expounded in the Upanishads, includes insects. The Jain sect wore a cloth across the mouth so as to prevent their accidentally swallowing and killing a gnat. An offering of wheat may, even today, be placed for ants around their nests. The Muslim Mughal emperors adopted these attitudes and on the grave of the Empress Nur Jahan (who was a Persian noblewoman) is written, supposedly at her request, a verse that may be translated:

“Do not decorate my grave with flowers or candles
Because the flowers may deceive the song birds
And the candle may burn the moths”

In tropical and subtropical regions the actual maintenance of an insect collection is, as many here will know to their cost, a difficult operation and this must have been a powerful discouragement to amateur entomology in Africa, Malaysia and other areas.

Interest in Lepidoptera undoubtedly has an aesthetic element. In feudal Japan many fine Tyuhu (or Chu Fu) (Illustrations of Insects) were prepared (Konishi & Ito 1973). In 1785 Moses Harris, the author of “The Aurelian,” exhibited a “frame of insects” at the Royal Academy, presumably amongst the paintings of Reynolds, Gainsborough, and others. Parts of insects have been used as decoration and adornment in all parts of the world; Japanese and Korean shrines of the 6th century were decorated with buprestid elytra. Today they are used, especially in those sections of society for whom other cheap jewelry is unavailable. In India butterfly wings or beetle elytra may be utilized, sometimes as earrings or as an ornament (Tikli or Tella) on the centre of the forehead; in South and Central America they are commonly incorporated into jewelry and ornaments; whilst in parts of Mexico living specimens of large Cerambycids, painted and attached to a small chain and pin, are sold by street traders as a moving brooch.

The decorative value of insects was appreciated by the illustrators of illuminated manuscripts. There are quite remarkable representations of various insects (and other animals) in fourteenth and fifteenth century manuscripts. Among the more unusual species represented are the water boatman (*Notonecta*), the carpet beetle (*Attagenus pellio* L.) the firebug (*Pyrrhocoris apterus* L.) and a burnet moth (*Zygaena*) (Crombie 1952, Hutchinson 1974). Insects have figured in sculpture in many epochs

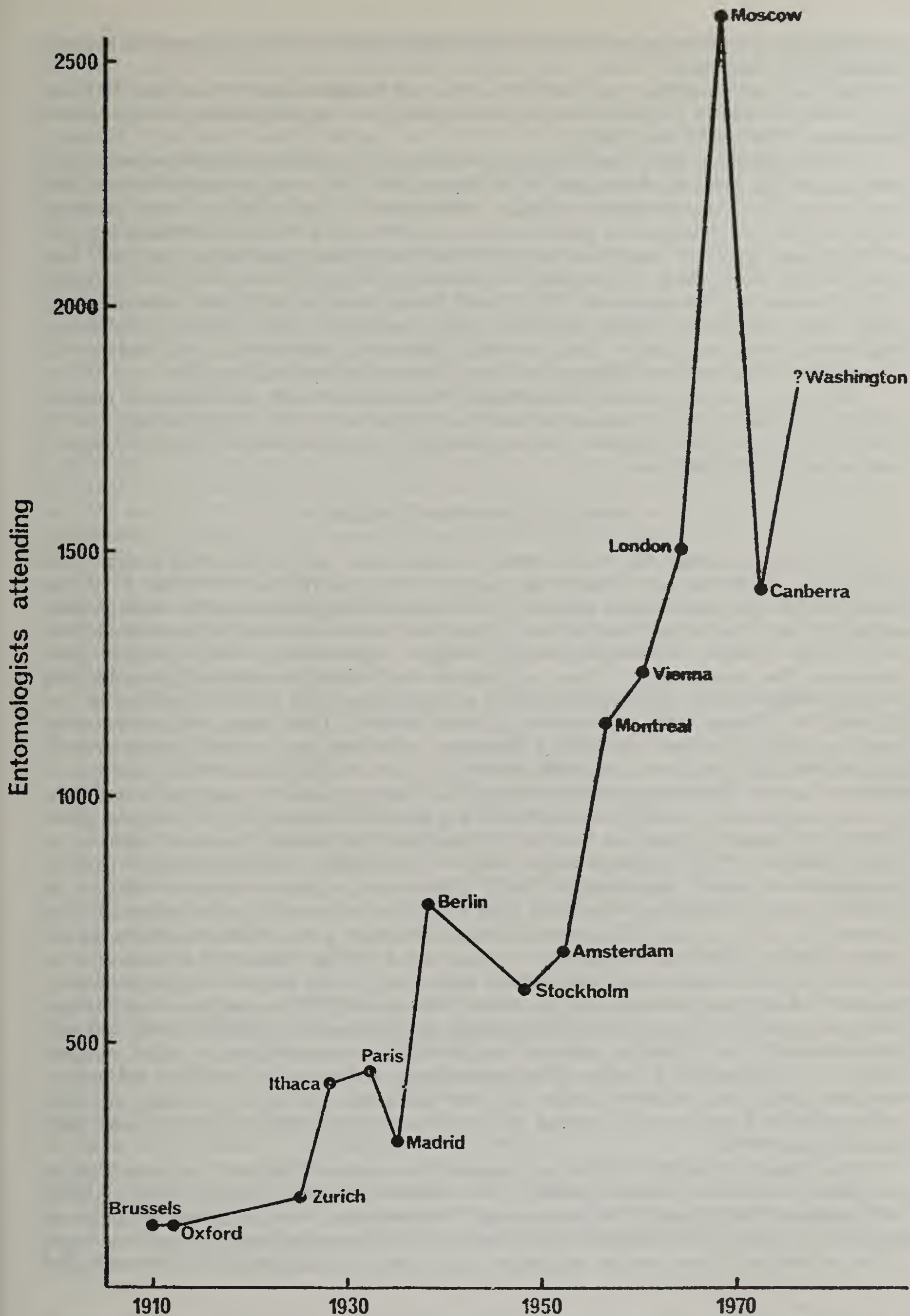


Fig. 2. —The number of entomologists attending International Congresses of Entomology.

and many areas: from Mexican terracotta fleas (200-800 AD) (Morge 1973) to the monarch butterfly at Pacific Grove, California!

Although various animals and plants have figured on postage stamps for more than 100 years (e.g., codfish and seal on the Newfoundland issue of 1866), it is only very recently that insects have been pictured* (Strom & Lewey 1968).

In 1930 Lebanon issued a series, figuring the stages of the silk moth (*Bombyx mori* L.) to commemorate the Sericultural Congress held in Beirut, after this it was not until 1948 that Chile issued a series (to commemorate the centenary, 1844-1944 of C. Gay's book on Chilean Flora and Fauna) that features *Chiasognathus granti* Stephens, a butterfly and a mantid. Since then many types of insects have figured on some hundreds of different stamps; sometimes whole series have been devoted to particular groups, for example, butterflies (e.g., Hungary 1959, Cuba 1965, Tanzania 1975) or beetles (e.g., Czechoslovakia 1962, Central African Republic 1962). Other issues emphasize applied aspects particularly malarial control (e.g., Dominica 1962, Ecuador 1963) or locust control (Mali 1964). Some (e.g., Japan 1966) are largely decorative, whilst France has featured the entomologist, J. Fabre and the USSR honored this Congress by a special issue in 1968.

One must conclude therefore that although the intellectual and artistic pleasure mankind derives from entomology is a comparatively small part of its role, it is very significant and with the spread of travel and the development of color photography and other relevant techniques, there is every reason why it should grow.

Insects and the Welfare of Mankind

Mankind undoubtedly first became aware of insects when they bit him! The genera of lice infecting man, *Pediculus* and *Phthirus* also occur on the apes (Buxton 1939) and so at that undeterminable time when *Homo sapiens* L. first became distinguishable his lice were probably making him itch! The medieval method a wife should use to de-louse her husband, described by Von Caub (1480), in Hortus Sanitatus, shows only marginal improvements on the technique of the chimpanzee (*Pan troglodytes* L.)! Fleas and bugs are less intimately and possibly less anciently associated with man; the more primitive forms of both groups seem to be ectoparasites on bats (Holland 1964, Usinger 1966). With bed bug (*Cimex lectularius* L.) it seems most likely that the transfer occurred somewhere in the Middle East region, when man was a cave-dweller (Sailer 1952, Usinger 1966): the Cimicinae are virtually restricted to cave dwelling animals: man, bats, pigeons, swifts and martins. There is no conclusive evidence that bed bugs transmit a disease and it seems that it is only comparatively recently, in the fifteenth and sixteenth centuries, that *C. lectularius* spread into Western Europe. [A pronotum found in a Roman site in Britain could, however, belong to this species (Osborne 1971)]. All these ectoparasites were widespread and often abundant until the development of modern insecticides in 1940-6. Tribute to the Aztec emperors of Mexico was sometimes paid in lice (Morge 1973). When Thomas Beckett was undressed, following his murder at Canterbury in 1170, his innermost garments of haircloth seethed with lice 'like water simmering in a cauldron' (Stanley 1906). Contemporary chroniclers, such as William Fitzstephen, who reported this regarded it as an additional sign of saintliness, so we may surmise that the size of the population was unusual for those times. However, even less than 40 years ago nearly 50% of the female children aged 2-13 and even 5% of the adults in a British industrial city had head lice (Mellanby 1941). Although these ectoparasites were ubiquitous mankind was clearly by no means indifferent to them: a Chinese pharmacopoeia of the second century recommends mercury and arsenic for the control of body lice, von Caub (1480) gives remedies for lice and fleas and perhaps the first professional economic entomologist was Londoner, John Southall, who ran a business controlling bed bugs and published a book on them in 1730.

Many insects are vectors of important diseases. The tremendous impact of epidemics of plague and typhus and endemic malaria on mankind are well documented (Bell 1924, Zinsser 1935, Barraud 1956, Brighetti 1968, Ziegler 1969, Scarborough 1970, Shrewsbury 1970, Garnham 1971, Glass & Reville 1972, Cipolia 1973, de Zulueta 1973, Harrison 1977). The magnitude of the impact of plague on the population of man must be emphasized: for example the pandemic of 542-594 AD killed

*A butterfly adorns the hair of Queen Liliuokalani on the Hawaiian 2c. of 1862 and a termite mound illustrates the 35c. Somalia of 1932.

about half the population of the Roman Empire, and a similar proportion were killed in England in the 'Black Death' (1348-9); these proportions compare with a death rate of under 6% in the most heavily affected areas in the First World War (Serbia and Montenegro) (Kosinski 1968). Typhus was the great killer when men were herded together and so armies were especially affected. The prevalence of malaria in ancient Rome, transmitted by the mosquitoes breeding in the surrounding marshes, is sometimes considered to have contributed to the fall of the Roman Empire (Celli 1933). Insect-borne diseases have also had their impact on history through the deaths of men of great influence: Alexander the Great seems to have died of malignant malaria and Oliver Cromwell died with quartan malaria (Garnham, pers. comm.).

Today insect-transmitted diseases are still widespread. It is estimated that at present 300 million persons in the World are suffering from filariasis, 200 million from malaria and 10 million from trypanosomiasis: thus about one in seven of mankind has one or the other of these particular diseases.* The magnitude of the importance of these insect disease vectors to mankind need not be elaborated and many papers at this Congress will be devoted to them. One should note, however, that recently some influential bodies are advocating a policy that emphasizes a biochemical attack on the pathogen itself rather than work with the vector (Dorozynski 1976).

An examination of the range of insects described by Aristotle (Peck 1965), by Pliny the Younger (Holland 1635) and by von Caub (1480) gives a clear picture of those noted by men in their everyday lives. The first group of the ectoparasites described above have literally been with man since prehistory. The second group, headed by the honey bee, concerned those insects that provided food, medicine wax and silk for man and the third group those that we would regard as pests: locusts, cankerworms and gnats, as well as woodworms and moths from 'wool and cloth when they be dusty' (Pliny, after Holland 1635). It is of considerable interest that at this time the number of insects regarded as useful seems to have been not much less than those noted as harmful: Pliny devotes nearly as much space in the Eleventh Book to the Honey bee (*Apis mellifera* L.), as to all other insects together. In contrast in 'Applied Entomology' (Fernald & Shepard 1921) over 80% of the pages that give specific accounts, refer to harmful species, although the authors note that "the benefits to man (of insects) are frequently overlooked."

The role of insects as sources of medicine, clothing and food has been diminished by new knowledge and new techniques. The Stag Beetle (*Lucanus cervus* L.) was unlikely to prove an effective remedy "against many maladies" as suggested by Pliny, but *Lytta (Cantharis) vesicatoria* (L.) is still recognized as producing a venom "howbeit medicinable in some sort" (Pliny). The major entomological work in ancient China was Li's (1596) Great Pharmacopoeia which gives a remarkable classification, as well as hundreds of medicinal uses (Konishi & Ito 1973).

The silkworms (*Antheraea*, *Bombyx*, *Philosamia*) have had an important role in the history of mankind from at least 4700 BC (Konishi & Ito 1973): silk was a major factor in encouraging trade and travel between East and West: Marco Polo (1294-1324) refers to it in the same way as silver and gold. The importance of silk is now much reduced, but in some areas, like Assam, every home will have a loom and it is part of a girl's upbringing to be able to weave silk.

The honey bee (*Apis mellifera* L.) is another insect whose importance to man has been recognized from the earliest times. Honey was a relatively more important food prior to the availability of sugar from cane (500 BC in India taking about 2000 years to spread to S.W. Europe) or from beet (1800 AD). Bee combs and honey gathering are figured in cave paintings from Spain, Australia, India and Southern Africa (Hernandez-Pacheco 1921, Pager 1973, 1976). Scutiforms, representing combs and ladders are common themes and those from Altamira, Spain are probably 20,000 years old. A rock painting from the Matopo Hills in Southern Africa clearly shows 'smoking a bee's nest' (Pager 1976). The importance of the bee was such that it became part of religion and lore (Edwardes 1911, Wheeler 1923, Ransome 1937, Townsend & Crane 1973). Reference has already been made to its representation in Ancient Egypt, but the hymenopteran depicted on the Minoan golden pendant is considered by entomologists to be a *Polistes* (Richards 1974). In medieval Europe the honey bee was still important; it is considered that the common heraldic symbol, the 'fleur-de-lis,' may represent a bee, head downwards: it is now used as the colophon on the Annual Review of Entomology (see Vol. 19, p. 5).

*At least one in six are suffering from some insect-borne disease.

Insects themselves were, judging from the ancient literature, more significant for food in the past than today. Aristotle (Peck 1965) advises that the male Cicadas are tastier when young, but the females are preferable later when they are full of eggs. American Indians and Australian aborigines also consumed cicadas. The latter often relied heavily on insect food including the honeypot ant (*Melophorus*) and the 'witchetty grub' (Hepialid and other large larvae) (Campbell 1926, Bodenheimer 1951). Even insect eggs may be eaten: in the lakes near Mexico City the eggs of various water bugs (Notonectidae and Corixidae) are collected on special rush traps and sold as 'ahualte,' whilst the adults are collected in nets, dried and sold as 'moschitos.' For a period John the Baptist probably depended entirely on insects for his food: 'he did eat locusts and wild honey' (St. Mark 1 v. 6). Large orthopterans are still an important item of diet, especially for children, in certain parts of Africa: locust control programmes need to take cognizance of this (Richards 1975) and various recipes for locust dishes are given by Abdullah (1973). The above are just a few diverse examples; entomophagy is advocated by Holt (1885) and the whole subject is well reviewed by Bodenheimer (1951) (see also Brues 1946 and Abdullah 1973).

Today our predominant concern in relation to insects and food is usually the food that they consume, although the role of pollinators, parasites and predators is not overlooked. Locusts are particularly spectacular defoliators and it is not surprising that their plagues have wrought wonder and anguish in the hearts of men from early times. They are shown eating cereals on a Mastaba erected towards the end of the Old Kingdom in Ancient Egypt (c. 2300 BC). Many of the ancient writers refer to locusts; often to various caterpillars and Pliny even mentions 'flies from radish roots and other little grubs likewise in lettuce and beet leaves' (Holland 1635, Meyer 1959, Harpaz 1973). Stored products pests, although not widely commented upon in contemporary writings, seem to have been widespread in ancient times (Solomon 1965, Osborne 1971, Burleigh & Southgate 1975).

Today the range and magnitude of pest damage to our crops is well recognized. The value of insecticides applied in a single year probably approaches \$2,000 million (Lewis 1977). Cramer (1967) estimated world crop losses at 10-15%. As about 20% of the ever-growing population of mankind is without an adequate food intake (Ehrlich & Ehrlich 1970) and insect losses tend to be heaviest in just the areas afflicted by malnutrition, we can claim that the proper practice of applied entomology has a vital role in the future of mankind (Pimentel 1975) (Fig. 3).

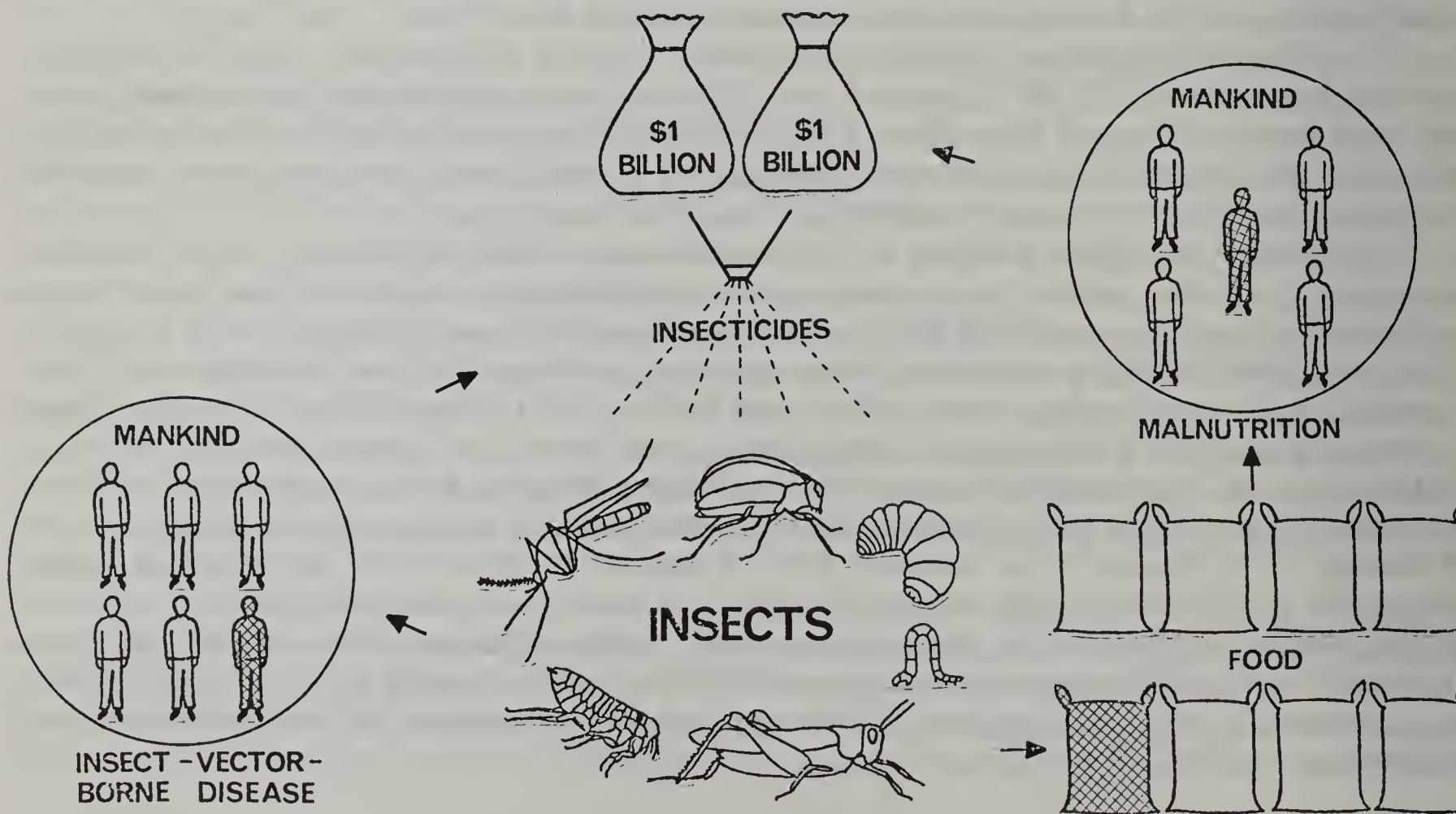


Fig. 3. — The impact of insects on the welfare of man.

The Co-existence of Mankind and Insects

After pointing out that about one in six of mankind is suffering from insect-borne diseases and that one in five is malnourished, whilst insects consume enough food to satisfy these needs, co-existence may seem an odd choice of words. You may feel McKelvey's (1975) concept of our task "to banish those insects which, as pests, are doing us more harm than good" is more appropriate. However, banishment or eradication must, I think, remain the exception rather than the rule: this is because the costs are too high. In this final section I wish to explore the strategy of this co-existence and from this explanation I believe the justification for my view will emerge.

Whether a particular species of insect has pest status in an area will depend on (a) its numbers and (b) the sensitivity or tolerance of the victim (crop, animal, person). From this it follows that an understanding of the principles that underlie the population dynamics of pests is an important component in a pest management scheme.

During the last few years progress has been made in understanding the essential dynamical features of insect populations (May 1976). Both single and multiple species systems may show a range of dynamic behavior depending on the magnitude and relationships of certain parameters in the relevant population equations (Hassell & May 1973, May, Conway, Hassell & Southwood 1974, May 1975, Hassell, Lawton & May 1976). The magnitude of certain of these parameters, intrinsic to the insects, are clearly the result of evolutionary selection; the templet for these, on theoretical grounds supported by the analysis of the life tables of 32 different insects, appears to be the durational stability of their habitat (Southwood, May, Hassell & Conway 1974, Southwood 1975, 1976). Durational stability is defined as H/τ , where τ = generation time and H is the length of time that the habitat location remains suitable for breeding. The H/τ spectrum relates to the r-K continuum (MacArthur & Wilson 1967, Pianka 1970). Basically those species with habitats of low durational stability are r-strategists: they tend to be small, mobile and with a short generation time. Species with

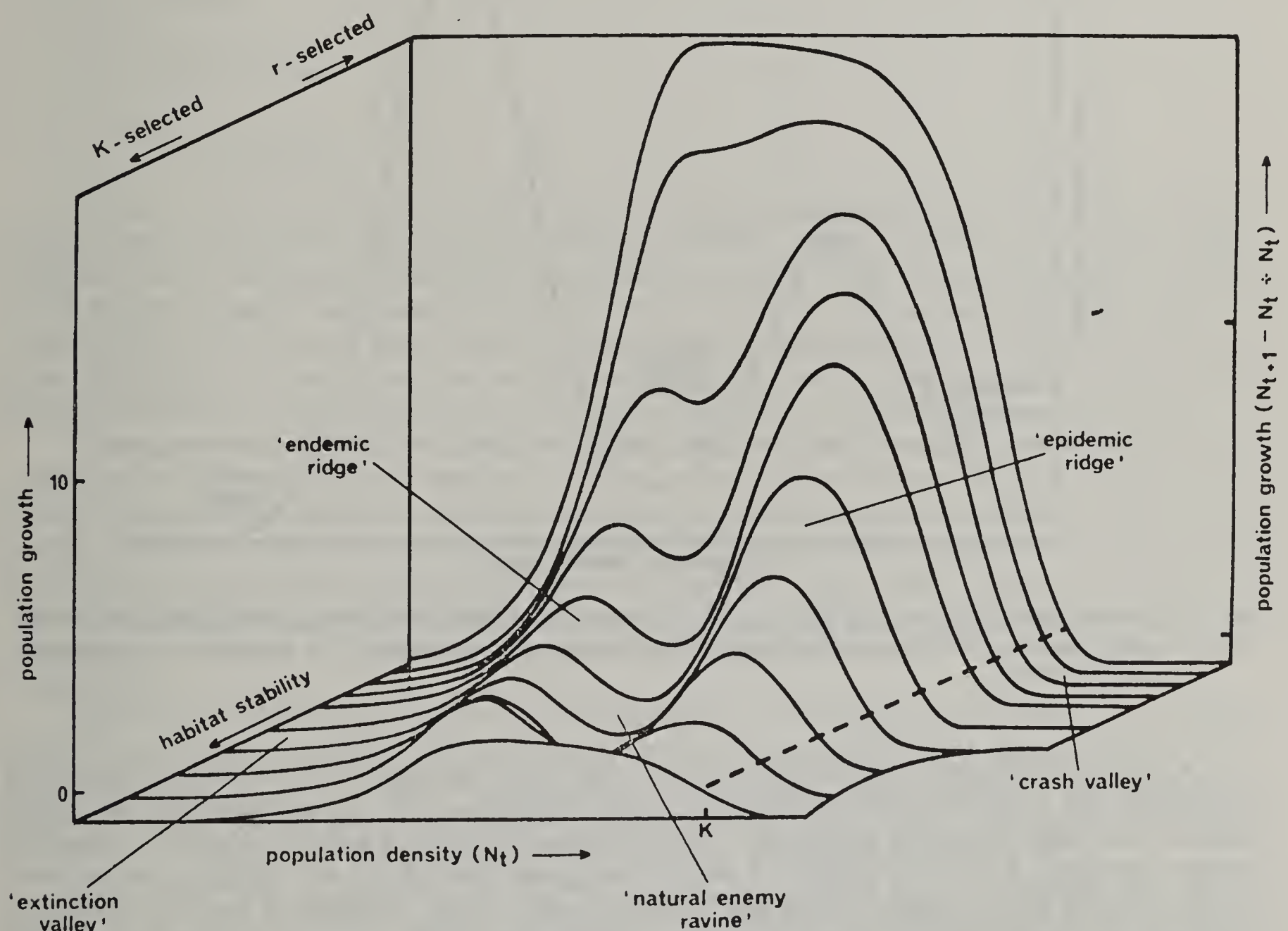


Fig. 4. —The synoptic model of population growth with axes for population growth, population density and durational stability of the habitat (after Southwood 1977).

stable habitats (high values of H/τ) are towards the K-end of the continuum, they are larger, more likely to be territorial than migratory and have a long generation time.

It is therefore possible to construct a three-dimensional synoptic model, that illustrates the basic features of population growth in relation to population density for species at different points in the r-K continuum (Fig. 4) (Southwood 1975, 1976, Southwood & Comins 1976). The precise position of a species on the r-K continuum is flexible and responsive to evolutionary pressures. The adjustments and readjustments depend on the processes of genetic feed-back clearly propounded by Pimentel (1961, 1968 and Pimentel & Soans 1971). An important feature of this model is the 'natural enemy ravine' that is deepest at the intermediate position in the r-K continuum and dips below the zero growth contour. This is because there are two stability points for the populations of these species: an upper one determined by competition and a lower one determined by natural enemies (Fig. 5) (Southwood 1975, Hassell 1976, Southwood & Comins 1976). Populations of, for example, forest insects often remain at comparatively low levels for much of the time: that is they are held in the domain of stability (Holling 1973) of the natural enemy stability point (S). However, from time to time an environmental disturbance allows the populations to escape from this equilibrium level, past the release point (R) and rise to a much higher density (U): an outbreak occurs. This is exactly the situation described by Clark (1964) for the eucalyptus psyllid, *Cardiaspina albitextura* Taylor, and its dynamics can be described in terms of this model (Southwood & Comins 1976). When the European spruce sawfly [*Diprion hercyniae* (Hartig)] was first introduced into Canada, its population, free of all natural enemy control, rose until limited by competition; but the combination of parasites and a virus disease reduced the population level (Balch 1939, Bird & Elgee 1957) and the lower equilibrium level was established (Southwood 1977).

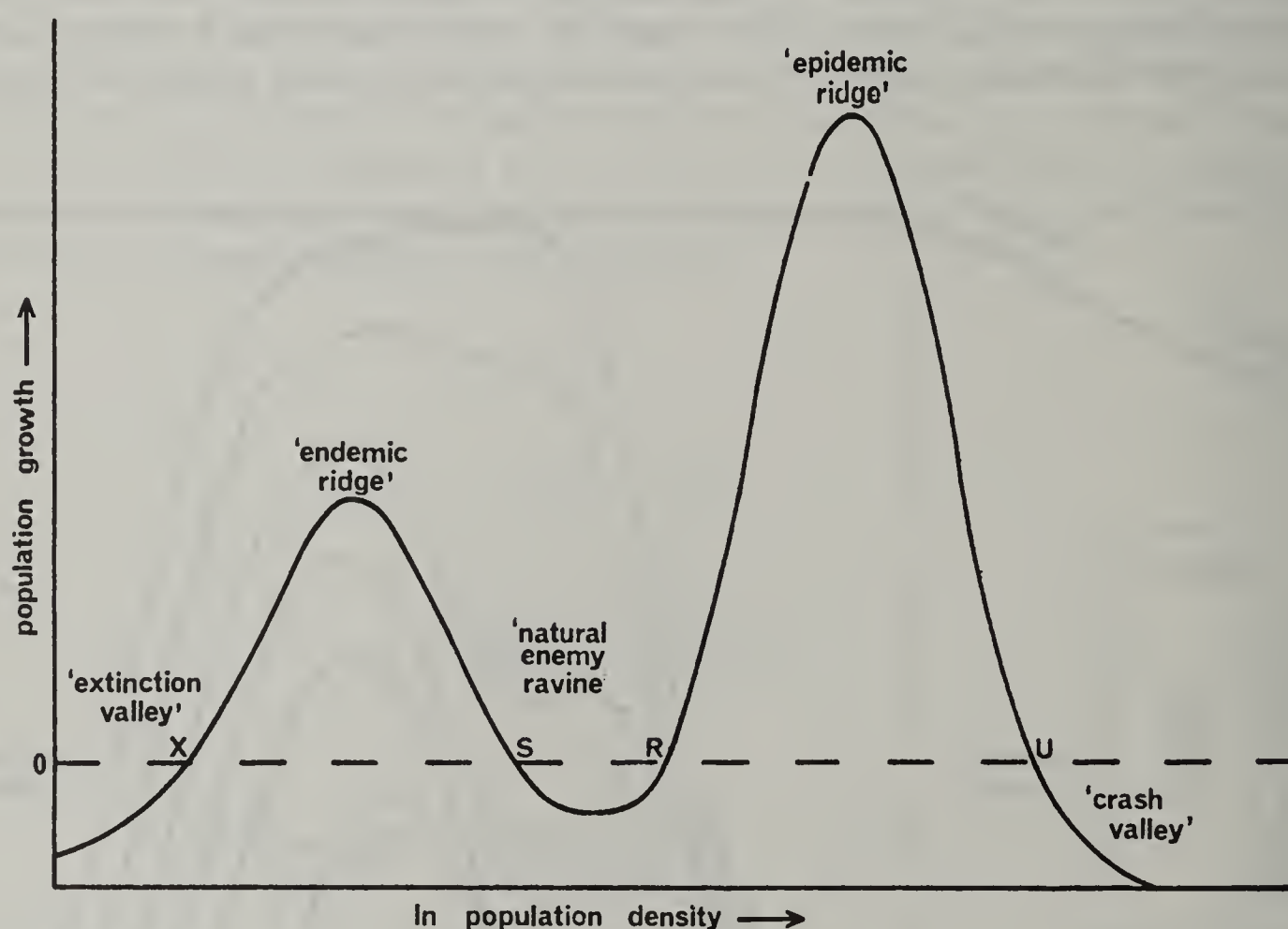


Fig. 5. —A section through the 'natural enemy ravine' of the synoptic model with two stable equilibrium points (S — natural enemies; U — intraspecific competition) and two unstable points (X — extinction; R — release to epidemic levels).

Conway (1976) has suggested that the concepts from this model may usefully be applied to pest species and I have been able to elaborate the idea (Southwood 1977). *r*-pests are characteristic of habitats with high durational instability — desert locust, *Schistocerca gregaria* (Forskl.), house flies (*Musca domestica* L.). Their strategy is one of boom and bust; the 'bust' holds no evolutionary penalty because that particular habitat location is no longer tenable, members of the species will have migrated and some will have found new sites (Southwood 1962). Natural enemies are of little significance, *r*-pests will virtually always achieve pest level if enough of them invade the crops and there is adequate time before harvest.

K-pests in contrast will occur in more stable habitats: their reproductive rates will be low and their population fluctuations will be small compared with *r*-pests. The codling moth [*Cydia pomonella* (L.)], the tsetse flies (*Glossina* spp.) and various large Bryocorine mirids that attack cocoa in West Africa and the Far East are typical examples. A *K*-pest's normal harvesting has no significant deleterious impact on the supply of its natural food, [n.b. cocoa is not the original host of the mirids (Leston 1970, Conway 1971)]. However, if this level of harvesting is intolerable to man, as codling infestation of apples is, then such species are virtually always pests.

In between these extremes are the majority of deciduous forest insects, fruit insects and some vegetable pests. These are for much of the time held at a lower equilibrium point by natural enemies, but when they escape from this 'natural enemy ravine' they reach outbreak level and become pests. Those near the *r*-end, like aphids, escape most frequently.

This knowledge we have of the basic underlying population dynamics of different pests gives useful indications of the appropriate pest control methods (Conway 1976, Southwood 1977) (Table 1): control being used in the sense of reducing the impact of pests so that the marginal cost of further measures will be more than the marginal revenue gained from the further increment in yield (Southwood & Norton 1973, Conway & Norton 1977).

Table 1.—Indications for control methods in relation to ecological strategies of pests.

<u>Control Method</u>	<u><i>r</i>-pests</u>	<u>Intermediate pests</u>	<u><i>K</i>-pests</u>
Insecticides	+++		++
Natural enemies.		+++	++
Cultural	++	+	+++
Reproductive		+	+++
Host resistance	++	++	++

r-pests are always fluctuating and therefore any appeal to the stability of natural ecosystems is spurious and foredoomed to failure (van Emden & Williams 1974, Southwood 1977, Way 1977). Cultural control techniques will depend on reducing the chances of pest invasion (Southwood & Way 1970) by, for example, increasing the scale of the monoculture and so heightening the degree of isolation (Way 1974). But in these inherently 'booming' populations insecticides will remain the most powerful technique: their rational use will demand the development of better methods of forecasting (Way & Cammell 1973, Benedek 1975) and assessing (Matthews & Tunstall 1968) pest outbreaks.

The appropriate strategy for intermediate pests will depend on maintaining them below their release point, in the domain of stability of the natural enemy equilibrium point (S). These are the pests where biological control or integrated control with a significant natural enemy component must be the dominant strategy (e.g., van den Bosch et al. 1971). The regular prophylactic application of insecticides to such pest systems will eliminate the natural enemy ravine: hence the outbreaks of 'secondary' or 'upset' pests (Entwistle, Johnson & Dunn 1959, Conway & Wood 1964) are consequences of such an ill-advised approach, called by Newsom (1975) a "womb to tomb" programme.

The *K*-pest will be most sensitive to the disturbance of its habitat; it will often have complex reproductive tactics and these with the low recruitment rate of the adult stage lead to a broad extinction valley in the synoptic model (Fig. 4). The majority of *K*-strategists fail to adapt to man-made environments, but those that have may be controlled by a variety of methods, particularly reproductive techniques involving sterile males or the use of pheromones (Roelofs 1975).

Host resistance is valuable for all pests; it may be thought of as decreasing the rate of population advance across the synoptic landscape. More precisely it reduces the finite natural rate of increase, the effect of which is shown in Southwood & Comins' (1976) simulations.

From this survey you will see that I consider insecticides are a vital tool in our co-existence with insects: we cannot do without them, but they do not provide the whole answer. When the

tactics of any particular pest control operation are being considered the cost of control is a major factor. The costs of an insecticide are:

- (i) the cost of the material.
- (ii) the cost of application.
- (iii) 'external costs' — their influence on non-target organisms, etc. (Langham & Edwards 1969).

Fortunately increasing attention is being paid to external costs; here in the USA, a legislative framework is developing (Deck 1975). The cost of insecticides themselves, in spite of recent increases, remains modest. However, the costs of developing new pesticides are fearsome, probably in the region of \$15-20 million at current prices, and there is clear evidence that the number of new products being introduced has fallen markedly (Lewis 1977). It is therefore in the interests of all concerned that the 'life' of the available insecticides should be as long as possible.

The useful life of an insecticide may be terminated by the widespread development of resistance in target organisms or by the saturation of the ecosystem so that non-target organisms are affected and the product becomes banned, as has happened in many countries with DDT and several other compounds. Many factors influence the development of resistance and the attainment of significant damage to the ecosystem, but in general terms they are both proportional to the quantity and the rate of usage of the particular insecticide (Smith 1970, Way 1971, Adkisson 1973, Comins 1976). Forecasting and the assessment of pest level, referred to above as well as new techniques (ULV, granules, etc.) that greatly reduce the quantity of insecticide applied per unit area (Kiritani 1974, Jepson 1976, Matthews 1976) are important in our attempts to prolong the life of an insecticide. Routine use and overkill must be avoided: the health dangers and the agricultural risks of a breakdown in the availability of insecticides are very great. This has been emphasized by Drs. Pal and Brown (1974) of WHO and by the recent National Academy of Sciences Committee under Professor Donald Kennedy (Carter 1976).

Against this background we can return to the question of banishment or eradication as it is commonly called. The basic characters of the population dynamics show that *K*-pests, with their wide extinction valley, are indeed vulnerable to eradication: especially by habitat modification. Unfortunately most *K*-organisms are just those we wish to conserve: many tropical rain forest butterflies and, extending beyond insects, birds such as condors and albatrosses. Other species will 'bounce back' from very low population levels and even if locally exterminated the remarkable dispersive powers of most insects, that are not at the *K*-end of the continuum, will ensure recolonization. Eradication programmes based on insecticides inevitably involve their heavy, widespread and prolonged use (Loftgren, Banks & Glancy 1975): experience has shown that because of this these programmes tend to squander a valuable resource — the life of the insecticide.

In conclusion as we look to the future one can see new vistas and an ever widening role for entomology in the service of mankind. We will continue to co-exist with insects using an increasingly sophisticated range of techniques. Pest management will develop a theoretical as well as an empirical basis. We will learn the lesson that pesticides are precious; their benefits may be so easily curtailed by wanton application. We must be precise not profligate in their use.

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Entomology and the Problems of the Tropical World

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ABSTRACT

In the address to the Closing Plenary Session of the Fifteenth International Congress of Entomology, the author re-examines the traditional view of entomology and rejects it as a restrictive one. He advocates a more concentrated attack on a deep understanding of insects in their ecology, physiology, genetics, relations and interactions with other living organisms, and other specialized facets of insect life, leading to a recognized "insect science and technology." In this respect, he believes that insect scientists and technologists should be concerned with "insect livestock" — just as they are presently concerned (and over concentrating) on insect pest management. Finally, he pleads for a recognition that the tropics is the original and preponderant home of insects, and that a study of insects must naturally mean a major study of tropical insects in situ.

As one reflects on the advances of the study of insects over the last thirty years or so, one becomes uneasily aware of the tremendous reputation the insects and their close relatives, the mites and ticks, have acquired as pests of man, his crops, and his livestock. The discovery of DDT, with its spectacular killing powers, its persistence, and its wide spectrum of insect targets, tended to put in the hand of man a new weapon of a bully — for clubbing to death all insects and sundry, friend and foe alike. It has become all too easy to regard any insect one meets with as a pest. Indeed, we have become brutalized in the course of our indiscriminate killing of our insect co-inhabitants of the Planet Earth.

"Entomology" is supposed to mean the study of insects in all the facets of their lives in relation to the environment, just as "ecology" signifies the study of living things in relation to their environment. Yet, there is hardly any professional entomologist who does not derive his primary livelihood through the killing of insects, or the study of how to kill insects, or the training of younger colleagues who will do the job for him in later years. We, the latter-day entomologists, are living a kind of apologia, in which we (or at least a majority of us) attempt to tell the world (and to deceive ourselves in doing so) that the principal reason why we devote so much intellectual capital in the study of insects is really in order to know how best to kill them. Perhaps we do.

But perhaps we do not really mean what we tell the world. We are like Pain (1953) who found the world of beetles much more engaging than there being regarded merely as pests. In his little book, *Lesser Worlds*, he describes beetles in almost poetic terms:

"There are, in fact, all kinds of beetles, pleasant and unpleasant. The varieties are endless and it is impossible to come to any general conclusions about insects differing as widely in their habits and their way of life. And yet, when all is said, one is left with a feeling of affection for beetles.

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One remembers the common black beetle of the garden, plodding laboriously through the soil, the shining beauty of the sweet-smelling musk beetle, the unassuming lady-bird destroyer of garden pests. One remembers the curious glow-worm switching on her light to draw her love to her side and discreetly extinguishing it again when he reaches her — although none knows how she does it; and the alarming Bombardier Beetle, defying his enemies with volleys of artillery accompanied by audible pops and puffs of smoke. Above all, in this remorseless savage world of the insects, one salutes the domestic virtues of that humble Dung Beetle, the *Sisyphus*, so attentive to his mate, so hard-working for his children.”

It would seem that the honest thing to do is to admit to the world (and to ourselves) that we do love to study insects for the sheer joy of trying to understand this fascinating world; and that, as a dividend arising from this knowledge, we are prepared to assist in the killing of or controlling that very small proportion of the total insect fauna that is directly harmful to us.

Estimates of the number of insect species known vary considerably. But in tropical Africa, which is one of the principal homes of insects in the world, it has been thought that there might be well over 3,000,000 species. Of that number, only about 0.3% are major pests of man, his crops and his livestock.

“Yet, this small number commands the most concentrated attention of mankind. To be a ‘dudu’ is almost synonymous with being a nasty, wicked, pestiferous being; it seems that to be a ‘duduman’ is almost as noxious. Yet, many of these dudus are not only beneficial to man (e.g. bees, insect pollinators of horticultural crops, insect predators of other dudus), most of them could not care less about our existence one way or the other” (Odhiambo, 1975).

A way out of this dilemma is for us to systematically compile a balance sheet for the insect species that we do know well:

- Are they harmful to us (or our crops and our other products)?
- Do they help us in any other way — like being eaten, like producing products that we like to use, and like protecting us from our enemies?
- Do they completely ignore us?
- Are they worth knowing? Does knowing them add to our total sum of knowledge of the world?
- What is the secret of the success of insects in the present tropical world?
- How much concern do we cause insects, and how much do we benefit them?

If we ask ourselves these sorts of questions, and set about getting solutions to the latter for entry into our balance sheet, then we will truly be transforming entomology into a mature science and its application — INSECT SCIENCE AND TECHNOLOGY.

This notion of entomology is not a common one. Indeed, our present preoccupations with the problems of food production and the major tropical diseases (such as malaria, trypanosomiasis, and filariasis), where insects play a major and often a crucial pestiferous role, bludgeons all our finer judgements into accepting only the debit side of the insect/man equation. Yet, we must endeavour to reject this traditional insect world-view; we must remove the blinkers from our eyes so that we can look at the whole landscape and the horizon yonder of the insect world. It was Fabre who first expressed in 1918 this naturalist’s truth in his inimitable manner in his book, *The Sacred Beetle and Others*:

“It is a good thing from time to time to wield the hatchet in the overgrown thicket of tradition; it is well to shake off the yoke of accepted ideas. It is possible that, cleansed of its obscuring dross, truth may at last shine forth resplendent, far greater and more wonderful than the things which we were taught. I have sometimes harboured these rash doubts; and I have no reason to regret it, notably in the case of the Scarabad. Today I know the sacred pill-roler’s story thoroughly; and the reader shall see how much more marvellous it is than the tales handed down to us by the old Egyptians.”

The drama of tropical human life in the tropics is the drama of co-habitation, the drama of “insect bite man,” and the drama of “man eat insect.”

The Insect/Man Interphase

One of the closest non-human associates of man is the louse. The latter has co-habited with or actually parasitized our ancestors since pre-human times. The various species of louse have become closely dependent on man; they have become restricted to human blood for their sustenance, and die

within a few hours of the death of the human host because they cannot live on the cold body nor can they fend for themselves in the open environment. There are also another 250 species or so of sucking lice, which are likewise found living exclusively on the blood of other terrestrial mammals (with the exception of the carnivores, the dog family, and the marsupials). Just as with the human louse, they spend all their time on the skin of their hosts. It is of great biological and sociological interest that each louse species is restricted to a single host species, or a few very closely related host species. Indeed, one can identify the species of a host by the kind of louse species it harbours.

One of the great attractions of the study of human lice is to obtain an understanding of the intimate relationship that has developed between man and his lice fauna in the course of the long parallel evolution of the two groups of living animals. The living human species, *Homo sapiens*, carries two species of lice — crab louse (*Phthirus pubis*) which inhabits the human body hairs, especially in the pubic region), and two closely related subspecies of body louse (*Pediculus humanus humanus*) and the head louse (*Pediculus humanus capitis*). The two latter forms are almost identical in morphological terms, but are easily differentiated according to their habits. While the body louse lives mainly on clothing, especially near to the skin, the head louse lives in the hair of the head. Under experimental conditions, the two forms can be successfully interbred; but under normal circumstances in its natural habitat the two forms have little opportunity for cross-breeding and the incidence of this must be regarded as very rare.

An intriguing fact is that, for practical ecological purposes, the human louse fauna regards the human body as a complete ecosystem. Firstly, as we have seen, the three forms have circumscribed for themselves three distinct micro-habitats (and the attendant ecological niches) within which they live, feed, and reproduce during their entire life-cycle. The crab louse is largely confined to the pubic region, a universally available micro-habitat; and it is therefore not surprising that the crab louse is nearly world-wide in distribution, as it becomes transmitted to others through pubic contact. It is, in fact, rather uncommon throughout its range, although it has become much more common since the beginning of the 1960's — which may well provide a running commentary on the changing social behavior patterns of mankind. While the other two human louse forms are transmitters of louse-borne typhus and relapsing fever, crab lice causes no other unpleasant surprises to its host other than the need for scratching produced by irritation through lousy bites. It is within the realm of speculative louse biology that the crab louse has co-evolved with man for so long, and from such early times, that it can safely be regarded as having attained a symbiotic or mutualistic relationship. In contrast, the body louse seems to be a comparatively recent insect associate: it is carried from an infested person to another through clothing (especially that worn next to the skin). Clothing is a relatively new invention of man, who, in any case, possesses a naked body that is only covered by hair in a few strategic areas. It is possible therefore that the body louse is a recent migrant from the closely related head louse, from which it has genetically drifted as a result of behavioural and other isolation mechanisms. An observation that may well support this hypothesis is that the body louse can act as a carrier of typhus (and also of relapsing fever) — although in the course of doing so the infected lice, which carry the causative agent of typhus, *Rickettsia prowazeki*, die of the consequences of harbouring the rickettsiae. The latter multiply in the louse's gut, invade the stomach epithelium, burst through it into the body cavity, which leads to a quick death to the infected lice. The head louse, on the other hand, is not a natural carrier of typhus or relapsing fever, although it can be experimentally induced to transmit these diseases.

The second line of evidence that the human louse fauna regards the human body as a complete ecosystem is to be found in surveys of lice resistance to DDT and other de-lousing pesticides. For instance, in surveys carried in 1951 among a large group of Korean military personnel, it was a routine procedure to dust each military clothing-ware with DDT before it was worn. A long series of tests showed that body lice developed high resistance to DDT, whereas head lice retained their normal susceptibility (Brown and Pal, 1971).

Just as human evolution over the last 2.0 million years or so has been distinguished more by changes in behaviour than in anatomy — the making of tools, the habit of eating the meat of vertebrates, food sharing, domiciliary design and construction, the habit of living in group settlements, and many other traits that became distinctly “human” in the course of time — so the evolution of human lice has taken a parallel orientation, being more in the nature of specialization to exploit the peculiar advantages of available micro-habitats (pubic region and the head), and the harnessing of new opportunities thrown up by the evolving man (for example, clothing).

Is it possible that one way of tracing the origin and evolution of man may well be to look at the

parallel evolutionary history of the human louse? If so, we should look for fossil lice where we are presently excavating prehistoric sites for *Homo sapiens*, *Homo erectus*, *Homo habilis*, and all other species of the genus *Homo* and related primate genera in the Olduvai Gorge (in Tanzania), Lake Turkana (in Kenya), and the Omo Basin (in Southern Ethiopia), which have produced rich finds in the last 20 years for piecing together the origin and evolution of man. If East Africa is indeed the cradle of mankind, is it possible that this region is also the original evolutionary birth-place of the human louse? An important characteristic of the social primates (other than man) is that the search for and picking of lice (and probably also fleas) from mates or individuals in a family group forms a large and important part of social communication and contentment. It is just possible that this lice-hunting formed a large part of the process of socialization of the original man — and gave him (and her) time during such sessions to plan the general economy and life of the emergent micro-society.

The human louse can be regarded largely as a co-inhabitant of man and, in a sense, his socio-ecological associate. The mosquito vector of malaria can certainly not be regarded in this light. Three-quarters of a century have gone by since a systematic study for the control of malaria was begun, and some U.S. \$30.0 million is being expended annually now to eradicate malaria. Yet, it is still the biggest killer of mankind. Although the early attempts at the control of malaria by the reduction of the size of the mosquito vector populations through larval control in the first quarter century, and the attempted control of malaria through the interruption of the cycle of transmission by a pesticidal attack on the adult population in the second quarter century, both led to the demise of malaria in several countries, some 500 million people are still exposed to the threat of malaria, and about 1.5 million of them die each year of this tropical scourge.

Why have we not exterminated *Anopheles gambiae* (with its 6 closely related sibling species) and *Anopheles funestus* (with its 10 sibling species), the principal vectors of tropical malaria, in all these years? They are small and delicate, and certainly invite the bully in us to crush and stamp on these seemingly weak enemies. Ever since we invented DDT and other alternative insecticides, we did have an era of euphoria when we confidently predicted the eradication of malaria; yet we find that none of the sibling vector species have been exterminated — indeed, none of the 3,000 species of mosquito have been exterminated in the last 50 years through the use of insecticides or larval control agents. Our exploration of anopheline eco-genetics, behaviour, and physiology has become much deeper and more refined, with the hope that we shall identify some weak link in the anopheline/parasite cycle that we can latch on and attack. But we have forgotten about a major element in this three-factor situation of insect/parasite/man of man himself.

A. funestus breeds in cool, clear permanent waters, sometimes heavily shaded by vegetation. It is therefore a “rural” mosquito vector for malaria in the African tropics, where it comes into direct contact with man through its habit of resting in houses. On the other hand, *A. gambiae* is a more “urban” or “industrialized” mosquito vector in the African tropics. It usually breeds in any shallow or small puddle of water, unshaded and of relatively high temperature. Public works carried by man for opening up new development enterprises is therefore an ideal vehicle for *A. gambiae* to spread into. Road-works, new dams, new wells, swamp clearings, new excavations, all offer ideal conditions for the rapid multiplication of this mosquito. Man has therefore unwittingly aided and abetted *A. gambiae* to spread itself widely in Africa wherever the new nations are endeavouring to introduce new industrial and urban developments.

While we continue to study, in great detail, the anopheline/parasite interrelationships, we must devote equal effort to the study of man himself in this complex syndrome. The work of the ICIPE in the last two years has shown quite convincingly that *Aedes aegypti*, a carrier of yellow fever, can be wiped out — or at least greatly reduced — in the ecologically isolated villages along the Kenya coast if we could frequently empty the earthenware pots, in which water is traditionally stored, and erase the footholds on coconut-tree stems, used for climbing the tree in search of the coconut fruit, which are both favoured by the domestic and peri-domestic mosquito populations for breeding. Yet we continue to invest a great deal of intellectual and financial capital in pesticidal control and genetic management strategies, simply because we are ignorant of the human social factors that perpetuate these insect infestations and how we can manage the factors for vector control purposes. As Gillett (1975) recently pithily remarked:

“Perhaps the cult of the elegantly simple explanation, the interpretation that is readily understood by all, has had its day. We deceive ourselves if we think otherwise. Malaria will not disappear by spreading oil on the water. Malaria will not disappear by spraying DDT on house walls. The mat of convenience may conceal the problem by bringing temporary relief but it will

not solve it; malaria will remain to re-emerge as soon as we relax our vigilance. It is not the parasites and the mosquitoes that are simple: it is we who are simple, at least in our attempts to interpret their ways. It seems incomprehensible to me that we can study these three-component systems and almost totally neglect one of them — man.”

Man is lousy, and abets mosquitoes in his search for technocratic development, and man also bites insect. He is part and parcel of the total biospherical environment — and he should study the world with that thought firmly in mind.

The Tropical World of Insects

The history of Africa, during pre-historic and recent times, has been shaped to a considerable extent by the impact of insects. A highly relevant case is that of the tsetse flies (*Glossina*), transmitters of the dreaded human sleeping sickness and livestock trypanosomiasis, and how they have affected in a very significant manner the history of pastoral peoples in Africa (Lambrecht, 1964).

Glossina species are presently confined to the African continent; however, fossil records of these flies have been found in Miocene beds in Colorado in North America; and their disappearance from elsewhere other than Africa may have been the result of inclement climatic changes, including glaciations. At about the time of the Miocene, certain branches of the primate order left the forest environment and took domicile in the savannah, which was probably spreading at that time due to the use of the newly invented fire-making. Later on, these new arrivals were to develop the highly competitive characteristics that would give rise to the species of the family Hominidae. It is thought that one of the factors that favoured these ground-dwelling primate species was the demise of other large ground-dwelling vertebrates through the ravages of trypanosomes in that ecological situation. In any event, when man and man-like creatures adopted their new micro-habitat they became subject to the attentions of the trypanosome vectors, tsetse flies.

Several million years later, a giant revolutionary step was taken by man in his economy by successfully domesticating cattle. It is known that cattle were already a feature of human economy in Africa by 5,000 B.C.: rock paintings depicting cattle can be seen in the Sahara by 3,500 B.C., and domesticated humpless longhorn cattle (*Bos primigenius*) were brought into Africa through the Sinai peninsula at least 7,000 years ago, where they interbred with the indigenous *Bos opisthonomus* in North Africa, where they then spread to West Africa. These descendants have, in the course of genetic adaptation over several thousand years, acquired a certain tolerance to trypanosomiasis, which enables them to resist the geographical strains of trypanosome parasites in West Africa. This measure of tolerance has been developed as a result of intermittent challenge with trypanosome-infected tsetse flies over a long period of time, but breaks down under conditions of environmental stress (such as the recent pasture shortage in the Sahel Region of West Africa) or in the presence of new strains of the parasites (for instance, when the tolerant “ndamna” cattle are translocated to East Africa). Thus, the movement of pastoral peoples in Africa, and the spread of pastoralist civilization in Africa, have both been circumscribed by the tsetse-fly belts.

Cattle owners realized very early (before the scientists “discovered” that tsetse flies transmit livestock trypanosomiasis) that their herds face heavy losses if they travel through *Glossina* country. They therefore avoided these areas, and confined cattle movement to fly-free corridors having water-holes along their course. In time, these water-holes became foci of cattle commerce and other trade activities, and permanent settlements grew up in these places. In time, Timbuktoo (in Mali) and Kano (in Nigeria) became the centres of commerce and learning including mathematics, astronomy, and science. Indeed, it may well be that the first written description of the pathogenesis of sleeping sickness may have been written in 1374 in Bamako (capital of Mali) by Ibn Khaldun, an Arabian historian, who reported the affliction of the higher classes in Mali by this disease (McKelvey, 1973). A passage in the ancient Arabic literature on this powerful and rich African empire, states that its King at that time, Mari Diata II died of this disease very quickly:

“His end was to be overtaken by the sleeping sickness which is a disease that frequently befalls the inhabitants of those countries, and especially their Chieftains. Sleep overtakes one of them in such a manner that it is hardly possible to awake him, He (the King) remained in this condition during two years until he died in the year 775 A.H. (A.D. 1373-4).”

It is possible that the early fall of the Mali Empire may have been due to human trypanosomiasis — a disease that almost completely wiped out livestock production in the present-day Mali Republic during the recent Sahelian Drought.

But this story is not confined to the historical times only. It is estimated that between 1896 and 1906 about 0.5 million people died in the Congo River basin of sleeping sickness, and in some villages visiting doctors found the few survivors too weak to bury the dead (Bloss, 1960). It is also estimated that, at the present time, about 25-30% of potentially useful livestock production areas in Africa is cut off from this human activity solely because of livestock trypanosomiasis.

We cannot, whether we like it or not, escape from regarding the insect world in tropical Africa as a bludgeoning presence there. We do not care for 0.3% of the miriads of insect species that share our tropical world — they are our enemies. The great majority we disregard (and they disregard us as well). But there may be a tiny minority that we should perhaps pay attention to. Lawino, the wife of Ocol in northern Uganda, sings a lament about death, and in her song she sings the praises of insects (p'Bitek, 1966):

“Her little ones are good children,
Obedient,
Loyal,
And when Mother Death calls
Her little ones jump,
They jump gladly
For she calls
And offers simsim paste
Mixed with honey’.
She says
My only child
Come,
Come, let us go.
Let us go’.
And eat white-ants’ paste
Mixed with shea-butter!
And who can resist that?”

We eat honey made by honey-bees; we harvest honey from ant honey-pots for children’s use and amusement; we boil and roast and fry locusts for our food during locust plagues; we trap the winged adults of our favourite termite species for our food; we use the giant-jawed termite soldiers as surgical chemically sterile instruments for circumcision; we use the silk of spiders’ nests and those of giant silkmoths for drawing pus under a boil; and we let the trilling cicada lull our young ones to sleep during the noon tropical hotness. I sometimes wonder why we have not yet harnessed some of our tropical insects to help us live a more satisfying life as our INSECT LIVESTOCK!

We have, to some extent, hunted our honeybees for their honey and wax; and in some countries, such as Tanzania and Botswana, beeswax is a major export crop. But the science of tropical honeybee is rudimentary, and the technology of exploitation (by burning out the bee-colony and plundering it) is crude and “kills the hand that feeds you.” We trap the alate termites by putting up a frame-covered structure on top of a termitarium and then simulate the fall and rhythm of rainfall, when they normally emerge in masses in certain seasons. We get to the queen by breaking open the termitarium and taking the queen from its royal chamber. Or, we simply wait until the alates are naturally swarming out of their mounds and we compete with the birds, the geckoes, and the pangolins in gathering together the fallen termites. We are, in fact, still in the hunting phase of our insect pastoral life — exciting but inefficient, active but lacking the finesse of deep knowledge of the science of insect livestock production that will lead to an equally sophisticated technology for economic harvesting and exploitation.

I believe that we need to devote as much effort towards an understanding of the candidate tropical insect species for the new discipline of insect livestock production.

Yet, the tropical insect world faces us with many problems of choices: we must find a way of survival through the time-bomb of insect pestilence, insect harassment of ourselves and what we possess, and their occasional nuisance value; but we must also begin to find ecologically and economically sound ways of exploiting the insect world to our own uses and comfort; and, finally, we could derive a great deal of intellectual excitement by a greater understanding for its own sake of the ways and byways of insects. I believe that the only option we have, which will serve our interest as part of the ecological complex of the Planet Earth, is to engage in all three fields.

The original home of the insect kingdom is the tropical zone. We must therefore, as part of an international scientific community, expect the leadership of this three-component enterprise of the insect world to derive its empathy, motivation, and direction from the in-situ tropical community.

Making such a decision is one thing; implementing it is another. To take one cogent illustration, if we are to establish a research programme for the study of the grassland termite, *Macrotermes bellicosus*, for the purposes of harnessing its productive potential for our uses, then we may find ourselves devoting almost as much effort and investment in this endeavour as we have devoted to the study of the cow in schools of veterinary medicine and veterinary research centres. We will have to study, in *Macrotermes* in great detail, its life-cycle, its reproductive rate, its composition and appropriate harvesting times, its pathology and diseases (how to cure them and how to prevent their diseases under high productive schemes), their utilization for eating, soil building, scavenging, and competition with other herbivores (such as cattle and wild vertebrate game), their biochemical composition and nutritional value, the genetics of breeding and how to obtain a uniform or predictable level of known quality, and so forth. I have yet to hear of someone thinking of a Faculty of Termite Medicine, although there is a distinct hope for a Faculty of Insect Science and Technology. I am informed that there is at least one Faculty of Entomology in the U.S.A.!

Prospect

What are the prospects for this new science and technology of insects? From what one can conclude from the tremendous and still growing literature on insect resistance to pesticides, insect refractoriness to genetic manipulation as a long-term mechanism for insect control, the rapid evolution of insect biotypes able to attack new crop varieties selected for their resistance to insect attack, and the vigorous spread of the fierce African honeybee in the Americas, the prospect for insects on earth is extremely good. They have so far proved their infinite capacity to use their genetic potential to survive whatever new weapons we have invented to tackle them; they have shown equal eco-genetic ingenuity to exploit new opportunities that are opened to them by the activities of man and other natural phenomena. They are still ahead of us in many ways: for instance, their ultrasonic acoustic language, but more so their complex chemical communication system, is something we became aware of only recently and of which we are still abysmally ignorant.

We have only domesticated less than 100 species of plants for our agricultural production, and much fewer species of trees for our forest industry. We hunt other plants and trees and aquatic weeds for our uses; and all in all, man probably uses something like 500 botanical species. We cannot yet talk of the domestication of plants by insects because we have not yet asked the appropriate question in this way; but in a remarkable sense the tropical termites have domesticated a whole group of fungi, which are now confined to termite "fungus-gardens" and seem to produce essential ingredients of their diet (in the fungal conidia) and may well assist the termites in maintaining an air-conditioned and highly sterile mound environment. But much more remarkable is the great variety of plants and lower plants that insects have exploited; indeed, there is hardly a species of tropical plant growing under terrestrial and freshwater conditions which does not harbour one or another species of insect. Many of the insect orders (such as Orthoptera, Dermaptera, Odonata, and Neuroptera) had long evolved in the epoch before the appearance of the flowering plants. With the evolution of the flowering plants, a new explosion of evolutionary development among the insecta was set in motion that is still continuing today.

The relationships between insects and their flowering plant associates can be intimate and literally breathtaking, such as the relationship between wasps and orchids. And, in analyzing some of these relationships, we have come to realize that not only is an insect's eye-view very different from that of our view, we cannot begin to appreciate the chemical dialogue between insects and their plant associates — which may well be a major factor in their successfully buttoning onto the flowering-plant's rapid evolution.

While the prospect for the future of insectkind is excellent, the prospect for the future of mankind is not all that bright. Our environment is becoming a load of self-inflicted pollution; we cannot grow rapidly enough the food we require to feed ourselves adequately; and our own physical development raises real problems about our public health. The problems are becoming more acute in the less developed countries which by and large happen to be located in the tropical zone.

One experiment in making an attempt to get the basic information on tropical insect science for solving the technological problems concerning insects (whether for pest management or for insect

livestock production) is the International Centre of Insect Physiology and Ecology (ICIPE), located in Nairobi, Kenya. It was established 6 years ago, and purposely located in a tropical developing country so that (a) it can work on tropical insect problems in situ, and (b) so that it can build up the scientific capacity of the developing tropical world in solving this type of problem in concert with the international scientific community. It has necessarily devoted its initial effort on a highly restricted list of insect problems — tsetse flies, tick vectors of theileriosis of cattle, the international moth migrant (the African armyworm), stem-borers, termites under the semi-arid savannah environment, and mosquito vectors. The impact of the findings of this small, multi-national, trans-disciplinary, development-oriented research institute is becoming to be felt in as varied a field as uterine reproductive physiology to termite chemical language, from the production of super-tick giants to the phenomenon of tropical aestivation.

We have so far, over the last several million years, lost the various fights to the insects. But we cannot yet despair of losing the entire battle — although we have now acquired a healthy respect for our earthly co-inhabitant. Perhaps, we have now reached a phase when we must search for the co-existence of man and insects. It is in this sense that the ICIPE (and other like institutes) may well give us the tremendous basic knowledge we need to lay down the terms for this co-existence and its *modus operandi*.

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Section 1: Systematics

The Diversity of Insects and the Dominance of the Land

Moderator: M. S. Ghilarov (USSR)

Geological History and Evolution of the Insects

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ABSTRACT

The first insects known are from the earliest part of the Upper Carboniferous. Eleven orders are represented at various levels within that Period, belonging to the Apterygota, Palaeoptera, and Neoptera Exopterygota. Seven of the orders are now extinct. In the Permian, 19 orders occur, including 3 belonging to the Neoptera Exopterygota. The early Mesozoic insect fauna was more nearly modern and in the Jurassic several existing families appear. Most of the Cretaceous families are still living and about half of the Tertiary genera are also extant. Social insects have been found as far back as the mid-Cretaceous (termites and ants), whereas others (wasps and bees) do not appear until the Oligocene.

My assignment in this symposium is to present an account of the geological and evolutionary history of the Class Insecta, as it is now understood. I believe this is an appropriate time and occasion of such a discussion. As a result of increased activity, paleoentomology has made notable advances in recent years. To a large extent this progress has been due to the unique research activity of Dr. B.B. Rohdendorf and his associates at the Institute of Paleontology in Moscow, not only in the field work but in technical publications. I think it is safe to say that our knowledge of fossil insects has more than doubled during the past 30 years.

In this account I will consider the nature and diversity of insects during each of the successive geological periods, beginning with the Upper Carboniferous.¹ However, since I will make considerable reference to extinct orders, it is necessary for me to explain my own views and policy on these highly subjective categories. Anyone who works with fossils finds that the more that is known about the extinct forms the more difficult it is to distinguish between the higher existing taxonomic groups, such as orders, suborders and even families. For many years there has been a marked tendency for students of fossil insects to name and designate new orders because of some unusual feature in a fossil, which often consists of an isolated wing or even a fragment of one. As a result, 52 extinct orders have now been named, mostly of course based on Palaeozoic specimens. Anton Handlirsch, who published extensively on fossil insects from 1906 to 1937, has been the chief contributor to this list. Many of these orders have subsequently been synonymized with certain existing orders or other extinct orders but others remain in the literature to confuse the general picture of early insect life. In my own work I no longer recognize as valid those extinct orders based on fragmentary material and I

¹ To avoid confusion it should be noted that the term "Upper Carboniferous" is used here in the traditional sense, corresponding to the combined Stephanian, Westphalian and Namurian Series. In the Fossil Record (Harland et al. 1967) the term is used as equivalent only to the Stephanian.

assign the species involved to an *Incertae Sedis* category, such as “Order Unknown.” My acceptance of an extinct order requires the knowledge of both fore and hind wings (in the case of Pterygota) and the nature of the head, including mouthparts. Applying these criteria to the extinct orders, I find only 9 that I believe deserve recognition. In order to indicate the positions of 9 extinct orders in the general picture of insect classification it is necessary for me to turn next to a brief consideration of the main lines of insect evolution.

Derivation of the winged insects from the primitively wingless Apterygota, now represented by the Thysanura, has been almost universally accepted since the beginning of the present century.² Similarly, the insects with complete metamorphosis, the Endopterygota, have consistently been thought to have been derived from the generalized Exopterygota. In 1923 A.V. Martynov in Leningrad, and G.C. Crampton in Amherst, Massachusetts (USA) independently and almost simultaneously proposed an additional, intermediate step in the evolution of the Pterygota.³ This assumed that the primitive Pterygota (now represented by the Ephemeroptera and Odonata), having restricted wing articulation, were unable to fold their wings back over the body at rest; these were termed the Palaeoptera, a division of the Pterygota. The remaining Pterygota, forming the division Neoptera, and presumably derived from the primitive Palaeoptera, developed a special sclerite (the 3rd axillary) and associated muscles in the articular area of the wing, which enabled the wings to be flexed backwards at rest. The advantage of this mechanism to the insects is obvious; it enabled them to hide more effectively in foliage, under logs, stones, etc. This concept of the main lines of insect evolution, proposed over 50 years ago, is now generally accepted as the model of insect evolution that fits the available evidence better than any other (Figure 1). How the wings and their flexing mechanism, as well as complete metamorphosis, evolved is another set of questions for which no generally acceptable answers have been given.

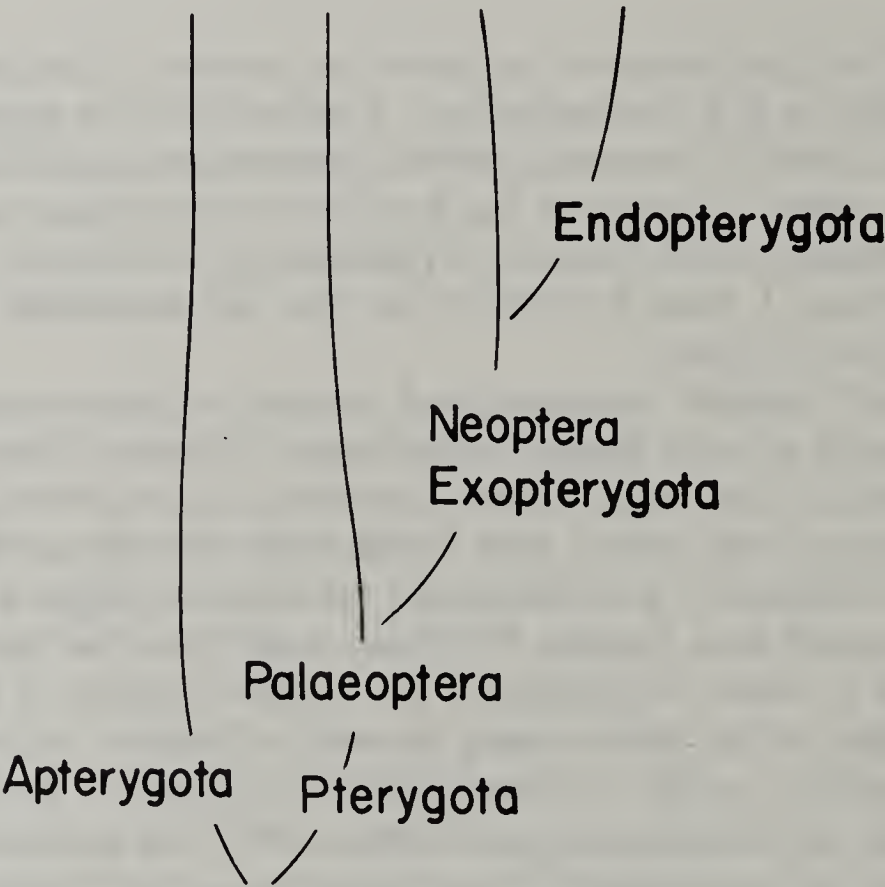


Fig. 1. —Diagram of main lines of insect evolution.

²Handlirsch, who considered the Thysanura secondarily wingless and derived from primitive mayflies, has been the chief exception (Handlirsch 1925, p. 363).

³Martynov elaborated on his conclusions in two subsequent publications in 1925 and 1938.

If we now return to the 9 extinct orders previously mentioned, we can place these with varying amounts of certainty in the present classification as follows:

Subclass Pterygota

Division Palaeoptera

Order Palaeodictyoptera

Order Megasecoptera

Order Diaphanopterodea

Order Protodonata

Division Neoptera

Section Exopterygota

Order Protorthoptera

Order Caloneuroidea

Order Miomoptera

Order Protelytroptera

Section Endopterygota

Order Glosselytroidea

Turning to the insect record of the Upper Carboniferous, a period of about 30 million years, we note that the Apterygota, Palaeoptera, and Neoptera Exopterygota were present at least part of the Period but that the Neoptera Endopterygota did not appear before the Permian. In the latter half of the Upper Carboniferous, above the middle of the Westphalian beds (Figure 2), there is a fairly respectable series of insects known, but in the early part of the Period, representing about 15 million years, only about a dozen specimens have been found. The oldest record of any insect consists of two

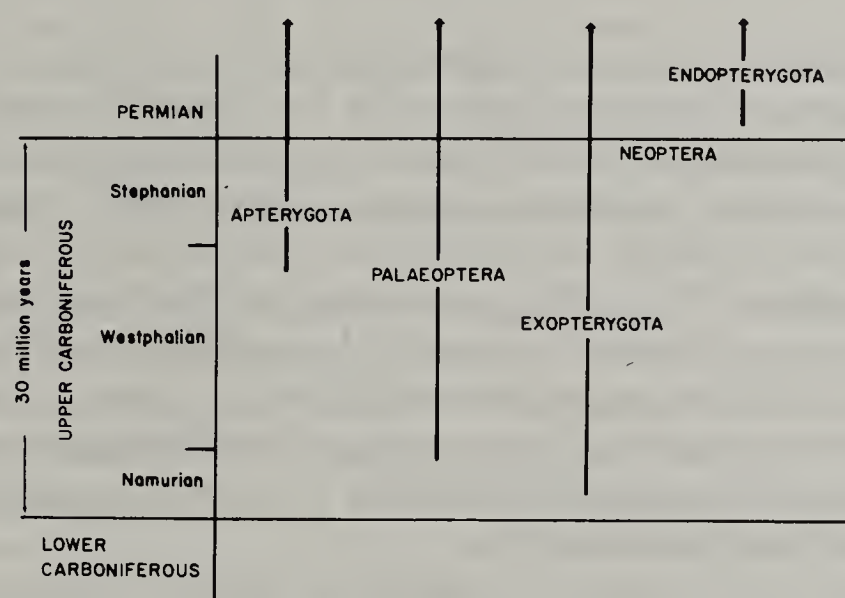


Fig. 2. —First records of major categories of Class Insecta.

isolated wings, one from Poland and the other from Pennsylvania (USA) in strata almost at the base of the Upper Carboniferous. The affinities of one of these is uncertain; it has been considered an exopterygote but it may in fact be palaeopterous. The sequence of the first appearance of the three groups, Apterygota, Palaeoptera and Neoptera Exopterygota, obviously has no phylogenetic significance because of the very small number of insects known from the early part of the Period.

Eleven orders of insects are known from Upper Carboniferous strata, as shown in Figs. 3 and 4. We will consider briefly the nature of each of these. The first Carboniferous thysanuran was actually described as a crustacean about 80 years ago and it was not until 1958 that its thysanuran affinities were recognized. At that time A.G. Sharov in Moscow found a similar species in Permian beds in the Soviet Union and recognized its insectan position. These specimens resembled the existing thysanurans of the suborder Machiloidea, the most generalized of the living members of the order, but they are even more generalized in some respects, such as the greater development of the limb vestiges along the abdominal segments. The feature that is unexpected in these Carboniferous species and that requires their separation into a distinct suborder, Monura, is the complete absence of cerci. Sharov was of the opinion that their cerci had been secondarily lost. However, the early nymphs of existing Machiloidea are remarkably similar to the monurans, having long caudal style and no cerci. As these nymphs grow, however, cerci develop and eventually reach at least half the length of the caudal style; in the more specialized Thysanura, the Lepismatoidea, the cerci become longer than the

style. Since Sharov's account of the Monura was published, more species have been found in the Upper Carboniferous of New Mexico and Illinois and the Permian of Kansas, Oklahoma, as well as of Moravia in Czechoslovakia. Some of these specimens are very small (although not as small as the early nymphs of Machilidae) but others are more than 30 mm. long (excluding the style) — but still lack cerci. Obviously, these are mature individuals, not early nymphs. It seems likely that these Monura represent a stage in the evolution of the Thysanura prior to the acquisition of cerci.

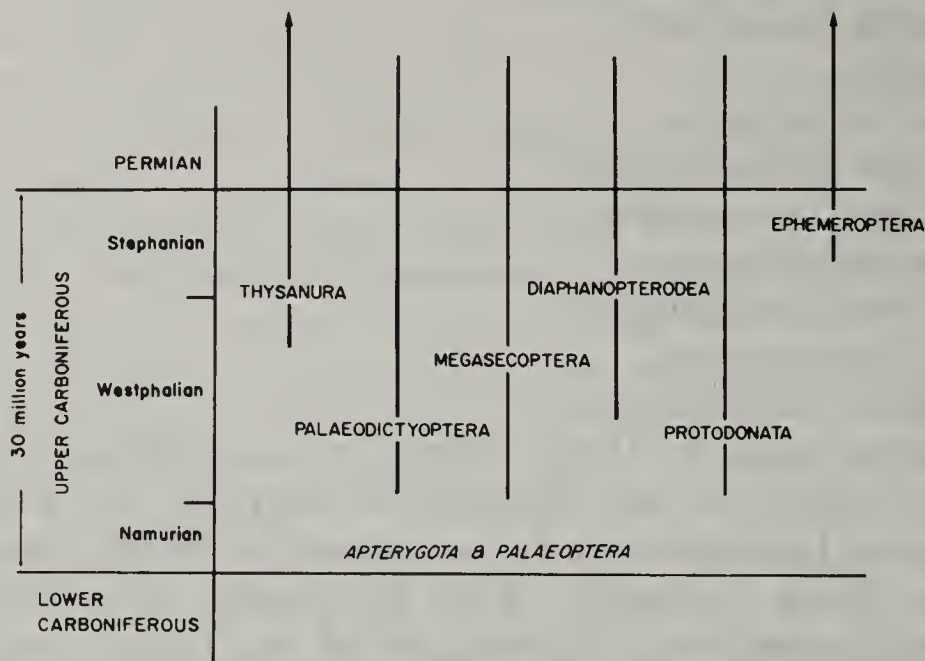


Fig. 3. —First records of insect orders in Upper Carboniferous: Apterygota and Palaeoptera.

Of the 5 paleopterous orders known from the Upper Carboniferous, 3 closely related ones were the dominant orders in terms of diversity; these were the Palaeodictyoptera, Megasecoptera, and Diaphanopteroidea. All were remarkable for their long cerci, prominent external ovipositors, and their specialized mouthparts: long beaks containing piercing organs, which presumably functioned as a haustellum. The clypeal region (probably the postclypeus) was enlarged, suggesting the presence of a well-developed sucking apparatus. The piercing organs within the beak consisted of 5 stylets, 2 of them paired and a median one, apparently the modified mandibles, maxillae, and the hypopharynx, as in the Lower Diptera. All of these insects presumably fed on juices of succulent plants such as the lycopods, that were abundant at the time. The nymphs of the Palaeodictyoptera and Megasecoptera were basically alike and possessed beaks like the adults. They were apparently terrestrial, since they lacked tracheal gills and other aquatic adaptations.

The Palaeodictyoptera were the most generalized of the three orders with respect to venation, although some specialized species had reduced hind wings and a few species had even lost the hind wings entirely — just as have some existing mayflies. The Megasecoptera had a more specialized venational pattern and the wings were often falcate, sometimes with reduction of the hind wings. The Diaphanopteroidea, although possessing the haustellate beak and a basic venational pattern like that of the two previous orders, were remarkable in another respect: they were able to fold their wings back

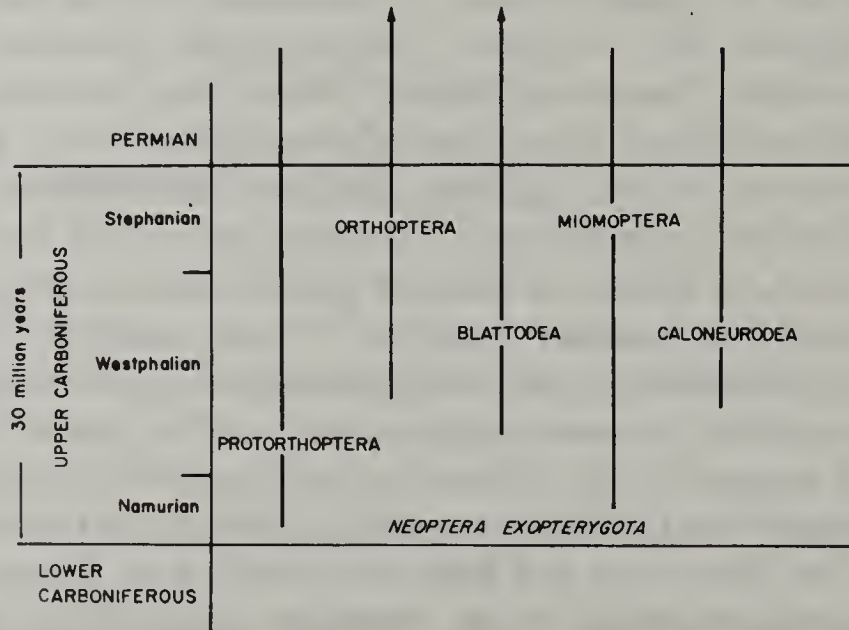


Fig. 4. —First records of insect orders in Upper Carboniferous: Exopterygota.

over the body at rest. Detailed study of their wing articulation has shown that this was not accomplished by means of the 3rd axillary plate, as in the Neoptera, although the precise mechanism is not clear. That these Diaphanopterodea were close relatives of the Palaeodictyoptera and Megasecoptera is shown by their wing venation and by the structure of the haustellial beak. The order was apparently much more diverse in the Permian than in the Upper Carboniferous and the Permian forms had a greatly reduced venation, although retaining the extraordinarily long cerci.

The Protodonata were undoubtedly close relatives of the true Odonata, but lacked certain venational features, such as the nodus, pterostigma and arculus. They were obviously aggressive predators and best known for their size; most species were about the size of large dragon-flies and some had a wing expanse of 750 mm — these being the largest insects known. Their nymphs have not been found; presumably they were aquatic. Along with the Palaeodictyoptera and Megasecoptera, the Protodonata apparently died out before the end of the Permian.

The Ephemeroptera is the only existing palaeopterous order known from the Upper Carboniferous. It is represented by one species with the venational pattern and other structures like those of the Permian mayflies, which are numerous in the record. The fore and hind wings of these Palaeozoic mayflies were homonomous and some of the Permian species, at least, had well developed, dentate mandibles. The nymphs of the Lower Permian forms were essentially like modern types, but had more tracheal gills.

Turning to the Neoptera Exopterygota of the Upper Carboniferous, we note that 3 of the 5 orders are extinct (Fig. 4). The Protorthoptera, the largest and most diverse of all the extinct orders, was an assemblage of species showing orthopteroid traits, such as the tendency for coriaceous fore wings, expanded anal area of the hind wing, prominent cerci, and of course mandibulate mouthparts. As presently conceived, this group may be a polyphyletic assemblage, but no one has succeeded so far in unraveling the evolutionary lines. The Protorthoptera seem to have been the earliest neopterous insects and were rapidly evolving and becoming adapted to diverse environments. Some had raptorial fore legs, other had large thoracic spines or projections, and venational patterns were extraordinarily diverse. That some of the existing orthopteroid orders evolved from early protorthopterous stock seems highly probable, though the order Protorthoptera itself apparently died out before the end of the Permian.

The extinct order Miomoptera consisted of small to very small insects, having mandibulate mouthparts, short cerci and homonomous wings. Not well known from the Upper Carboniferous they are very numerous in some Permian deposits, out-numbering representatives of all other orders. Their venation recalls that of the Psocoptera in some respects but their body structure is more like that of the Protorthoptera. This group also seems to have become extinct before the end of the Permian.

The order Caloneurodea is another enigmatic group. The fore and hind wings are long and virtually identical, the venation orthopteroid, but with some curious specializations; the mouthparts were mandibulate and the cerci very short. The general consensus seems to be that they are within the orthopteroid complex. Like the previous extinct orders, this appears not to have survived beyond the Permian.

The true Orthoptera (Saltatoria) are well represented in Upper Carboniferous, the modified hind legs being diagnostic. Their venation was basically like that of the existing Orthoptera and there is no obvious reason why these should not be considered the early stock that led to the present-day families.

The Blattodea of the Upper Carboniferous had already attained the characteristic features of the order: flattened body, tegminous fore wings, short cerci, and long antennae, with the distinctive venational pattern of the modern roaches. Surprisingly enough, however, the females in the Upper Carboniferous had long, external ovipositors, which certainly could not be used for depositing the oothecae of modern roaches. Whether or not all females in the Upper Carboniferous possessed such ovipositors is not clear, but in any event the ovipositors persisted in some roaches through the Permian and well into the Mesozoic.

From this survey of the 11 orders known in the Upper Carboniferous it is clear that the insects had achieved great diversity by the end of that period, some 280 million years ago; and that the Palaeoptera, Neoptera Exopterygota and, of course, the Apterygota must have begun their evolutionary development in the Lower Carboniferous.

In the Permian Period, which had a considerably longer duration than the Upper Carboniferous, 19 orders of insects have been found, 10 being new ones not present in the previous period (Figs. 5 and 6). Of these 10, all but 2 are still living. The one remaining palaeopterous order, the Odonata,

occurs in the early Permian, with two distinct types, representing the anisopterous-like lines and the zygoterous-like lines, although virtually nothing is known of their body structure. In the Neoptera Exopterygota four additional orders occur. The Perlaria are represented by forms very similar to the existing Eustheniidae. The extinct order Protelytroptera, apparently related to the Blattaria and Dermaptera, had well developed elytra and broad hind wings, which were folded up under the elytra at rest. In some species the elytra were sculptured in ways very suggestive of beetle elytra. The hind wings, however, had a venation similar to that of the Dermaptera, and very different from that of the Coleoptera. Combined with the presence of short cerci, the venation clearly eliminates the Protelytroptera from the Neoptera Endopterygota.

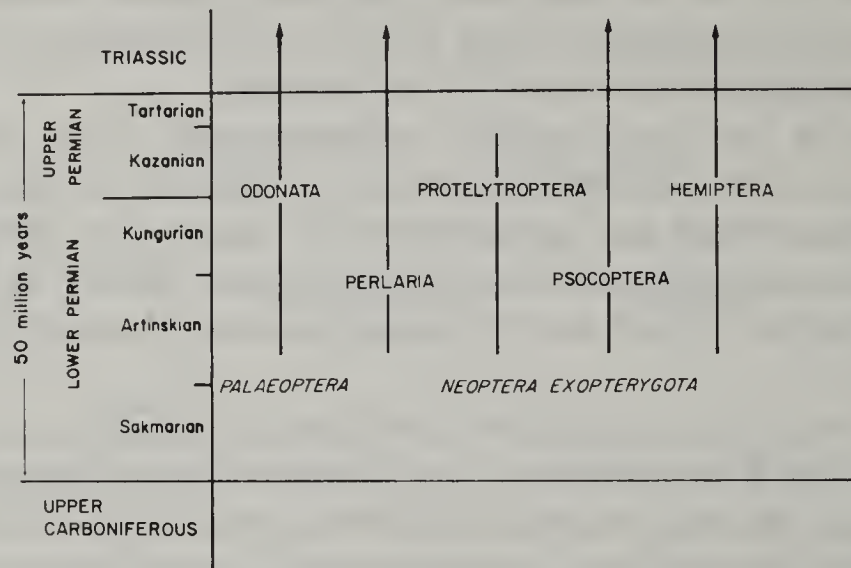


Fig. 5. —First records of insect orders in Permian: Palaeoptera and Exopterygota.

The Psocoptera are well represented and even very abundant in the Permian. Their wings were homonomous, with a venation showing some hemipterous features. All of the known Permian Hemiptera belong to the suborder Homoptera and include a surprising array of extinct families, some of which included species with long ovipositors. The characteristic homopterous beak was well developed, indicating that, like the Palaeodictyoptera and their relatives, the Homoptera had found an abundant source of liquid food.

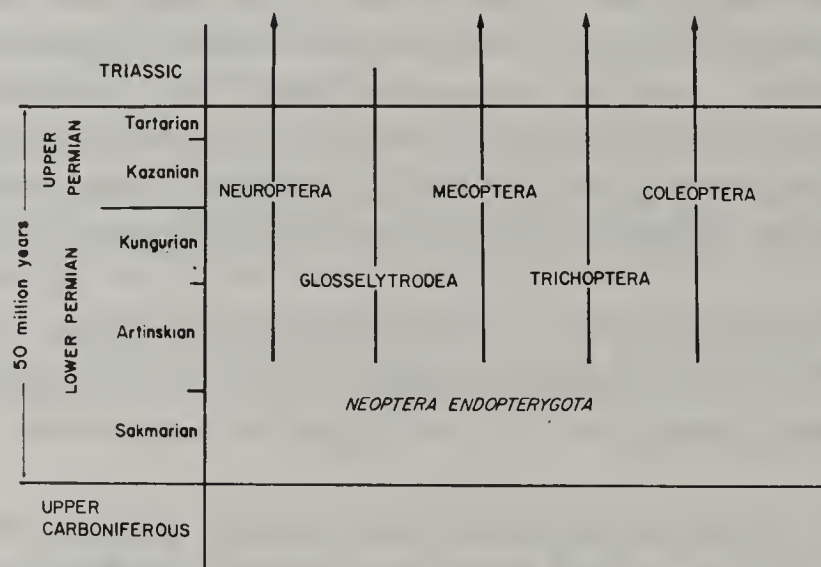


Fig. 6. —First records of insects in Permian: Endopterygota.

The most striking feature of the Permian insect fauna was the presence of 4 existing orders of Endopterygota — the Neuroptera, Mecoptera, Trichoptera, and Coleoptera. The Mecoptera were surprisingly diverse and included many more families than exist at present. The Permian Neuroptera comprised the suborders Sialodea, Raphidiodea and Planipennia. The Trichoptera were apparently diverse and had a distinctly generalized venational pattern. Only one endopterygote larva is known from the Permian; this is a sialoid and is strikingly like some of the existing ones. The first Coleoptera of the Permian are mainly primitive types with suggestions of an elytrous venation; apparently belonging to the Archostemmata, these remained dominant until the Jurassic, when an assortment of more modern families appeared, including some still existing.

The Glosselytrodea is the only extinct order that appears to have belonged to the Neoptera Endopterygota. The venation is much more specialized than that of the Neuroptera or Mecoptera and the fore wings are almost elytra. However, the trichiation of the wings and the general form of the head and thorax are strongly suggestive of the Neuroptera.

The Permian insect fauna was obviously much more diverse than that of the Upper Carboniferous. It included such very different types as the Palaeodictyoptera and Megasecoptera along with the Hemiptera, Mecoptera and Coleoptera. In terms of diversity of form and the association of generalized and specialized species, the fauna of the Permian was probably the most diverse in the history of the Insecta.

The most notable feature of the Mesozoic fauna was the apparent absence of the extinct orders of the Paleozoic; 17 orders are known in the Jurassic, 2 less than in the Permian (Fig. 7). Only the Glosselytrodea seem to have persisted into the Mesozoic and that extended only into the very early part. Actually, only a few insects are known from the Triassic, although some primitive Hymenoptera and Diptera have been found. By the early Jurassic, with the addition of the Dermaptera, Phasmatodea and Thysanoptera, and with the loss of the extinct orders, the fauna was essentially a modern one, with the presence of existing families in several orders, such as the Odonata, Orthoptera, Diptera and Hymenoptera. The long Cretaceous Period, which is distinguished by the rapid evolution of the flowering plants, has yielded very few insects until recently. Discovery of extensive amber deposits of Cretaceous age in Canada, Siberia, and Lebanon have now provided an excellent source of insects from a very critical time in their history. The Lepidoptera, previously known only as far back as the early Tertiary, are now represented by several primitive families from the mid-Cretaceous. The Isoptera, although not yet found in this amber, are also known from mid-Cretaceous deposits. However, it is to our knowledge of the evolution of families that the Cretaceous specimens will make their major contribution.

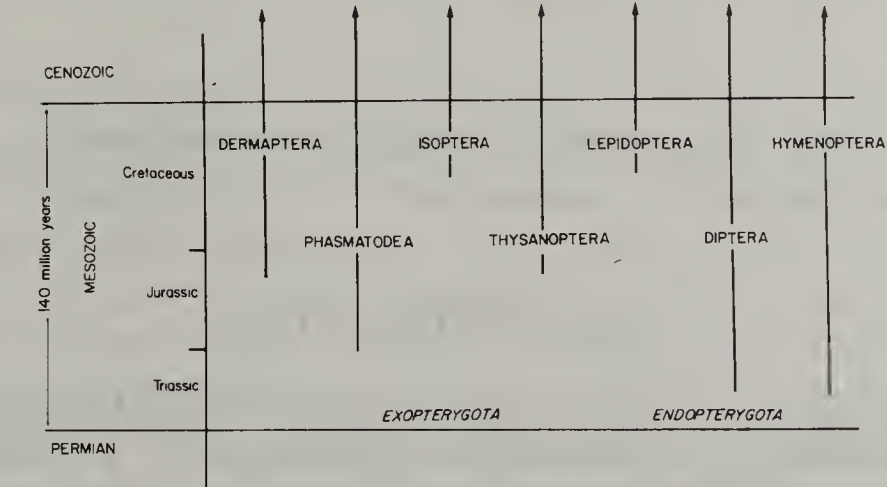


Fig. 7. –First records of insect orders in Mesozoic: Exopterygota and Endopterygota.

The Cenozoic has provided the first specimens of four additional insect orders, all occurring in the Baltic amber, which is of Lower Eocene age: the Mantodea, Embioptera, Siphonaptera and Strepsiptera (Fig. 8). The species, though extinct, are of present-day types. On the average, more than half the described Oligocene insects belong to existing genera and in general the extinct genera are no more primitive than the existing ones.

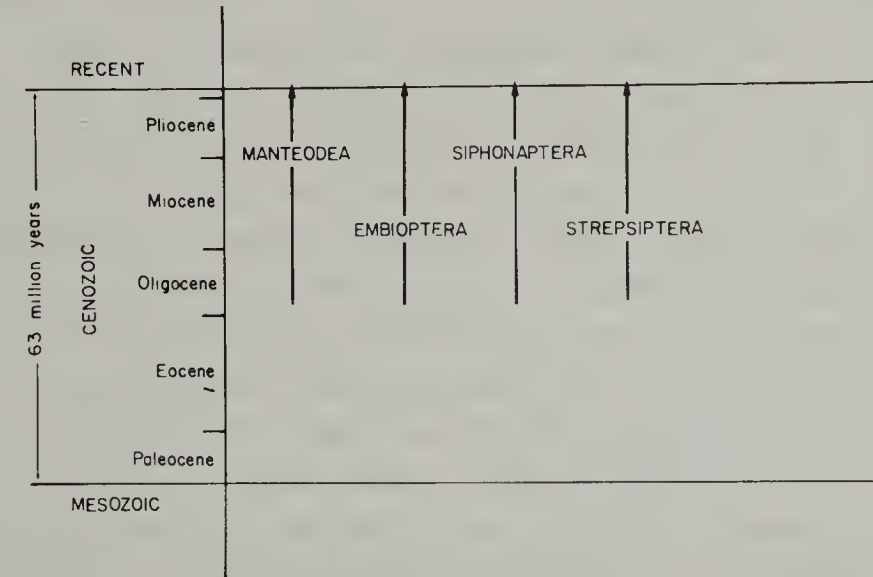


Fig. 8. –First records of insect orders in Cenozoic.

One of the most interesting contributions of the Cretaceous and Tertiary fossils is to our understanding of the antiquity of social behavior in insects (Fig. 9). The presence of a member of the Hodotermitidae in the mid-Cretaceous of Laborador indicates that the social habits in the order Isoptera had developed at least by the early Cretaceous. Social wasps, (Vespidae) are known from the Upper Oligocene of Germany, although there is no way of knowing to what extent their social behavior had been developed by them. The social bees have had a similar history. A true *Bombus* is known from the Miocene and true *Apis* have been found abundantly in upper Oligocene deposits. The ants have a longer history. Workers have been found in Cretaceous amber in the United States and the Soviet Union, extending these highly social insects back about 100 million years.

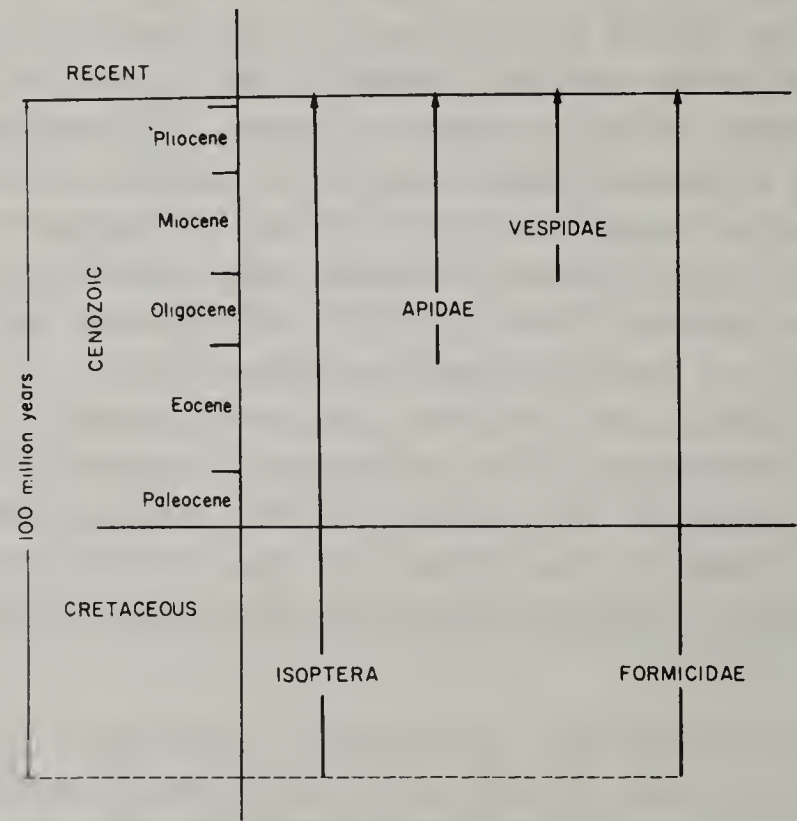


Fig. 9. —Geological records of social insect groups.

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Enabling Mechanisms

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Introduction

When the evolution of any group of animals is well-known, it is usual to find that the acquisition of its characteristic structures and habits occurred slowly and progressively up to a certain critical point, when, some acquisition being now perfected, the group was able to radiate rapidly because it could now exploit its previous environment more fully or because it could now invade environments from which it was previously barred. These critical points in evolution may be called nodal points.

In the evolution of insects there are four particularly striking nodal points. The first of these is the development of a tracheal system that enabled them to localize to some extent respiratory and humidity exchanges with the ambient air. The development of a tracheal system paved the way, so to speak, for the second nodal point, which was the acquisition of a more or less impermeable outer cuticle that enabled them for the first time successfully to invade dry terrestrial environments. The third nodal point occurred when lateral extensions of the meso- and metathorax, that had been used first for attitude control in falling and then for gliding, evolved into flapping wings so that sustained flight was for the first time possible. This third nodal point occurred in the early middle or lower Carboniferous. A short time later, geologically speaking, the developing wings were invaginated into the body of the larva and the last instar larva evolved into a pupa. This occurred after the end of the Carboniferous in the early Permian. The intercalation of a pupal stage in the life-history for the first time permitted insects completely to dissociate the form and structure of their feeding stages from that of their reproductive and distributive stages, and, as one consequence of this new capacity, there are few environments that are not exploited by insects. The great majority of insects have a pupal stage, and from the point of view of numbers of species they are far the most successful group of animals.

The success of insects, like that of any other successful group, is not to be attributed to any single factor but to a number of factors that together enable them successfully to deal with the difficulties imposed by very different kinds of environments. In addition to the nodal points mentioned above, two other important factors that contribute to the success of insects should be mentioned: their favourable size range and the evolution of a fat body. Insects are large enough so that they are not imprisoned by surface tension forces; many make great use of these during locomotion. At the same time they are small enough so that they can fall to any distance without injury. I know that a few Orthoptera with ripened eggs can burst if they fall onto a hard surface, but this sort of thing is very exceptional. Preoccupation with what, from one point of view, might be called secondary functions of fat body cells has drawn attention from the selective pressure that originally led to the development of this tissue. The development of a fat body distinguishes all terrestrial arthropods from primitively aquatic ones: storage of reserves of fat make it possible for them to sustain slightly longer periods of water deprivation than storage of reserves as carbohydrates or proteins, a capacity that in the long run would seem to be of very great selective value. The total

amount of depot fat of arthropods is correlated to the humidity of their environment: aquatic insects have far less fat than their close terrestrial relatives (Hinton 1953).

Insects evolved as terrestrial animals, and the tracheal system is an adaptation to life on land. In the past those who held that insects were primitively aquatic based their views on assumptions, the gratuitous nature of which has been discussed by Lemche (1940), and there is no need for me to repeat his arguments here. In giving me my terms of reference, one of the organizers of this symposium in speaking of insects said, "How did they originate and why have they not been able to return to the sea?" It is possible to attempt to answer the first part of this question. The second part of the question ". . . why have they not been able to return to the sea?" is very easily answered. They never had anything to do with the sea, neither insects nor their remote ancestors. I did not know anyone held such views these days, although from time to time one meets people who despite all evidence to the contrary still think that life originated in the sea.

Insects have not colonized deep waters to any extent, either sea or freshwater. I do not think that the intertidal area presents a serious physiological problem to insects, apart from some salt marshes where very high salinities may be temporarily reached. But the gratuitous assumption that the sea presents a more serious physiological problem to insects than freshwater has dominated thinking in this field for a long time. It has led to such absurd conclusions as those of Cheng (1976, e.g., p. 3), "Perhaps the physiology of the muscular or nervous system of an insect is so specialized that it cannot tolerate physico-chemical conditions like those of seawater."

In their important papers on this subject both Buxton (1926) and Mackerras (1950) came to the conclusion that it is simply the physical violence of intertidal areas that tends to exclude insects. I agree completely with this point of view. But I think we can go further than this. If the total available coastline is compared with the total available length of flowing and often violent freshwater, the argument is turned upside down: flowing freshwater have far fewer kinds of insects per unit area than the intertidal zone. Perhaps none will quarrel with the view that there are more than 400 kinds of intertidal insects and perhaps as many as 1,000. Now there are something like 17,000 freshwater insects of which about 10,000 occur in streams and rivers. The Amazon (+Solimões) is about 4,000 miles long, and in the Amazon basin there are some 30,000 miles of navigable rivers. If we add to this the lengths of the rivers and streams entering these, I would guess that the total length of all rivers and streams in Brazil is at least two orders of magnitude greater than the length of the main Amazon river. The coast of Brazil, however, is only 4,281 miles long. This is two orders of magnitude less than the river system of the country. I think that this kind of relation between coast line and river systems will, on the average, be of the same order as that for Brazil. The total coast line of the United States is only 13,400 miles and that of mainland Australia is only 16,000 miles. These figures are of course based on "smoothing" coastal and river margins in an arbitrary way. But if there were only 400 kinds of intertidal insects, there should be some 40,000 kinds of insects in flowing freshwater, whereas in fact there are hardly 10,000.

In speculating about the evolution of a group of animals it seems evident that the most basic and far-reaching mistakes that can be made consist of incorrect assumptions about the attributes of the environment in which the group evolved. The most serious mistake that is usually made is to choose as the environment in which insects were evolved either water or land and to consider these as sharply opposed because the land is thought of as dry. But from the point of view of moisture content, many terrestrial environments differ little from aquatic ones: they are saturated most or all of the time. In most climates many terrestrial insects are alternately dry and flooded. To be submerged in water for several hours or even days, a period that may, for instance, exceed the duration of the egg stage, is not a rare or isolated event but is a normal hazard of their environment. When this characteristic of terrestrial environments was first clearly realized it was possible to ask a question that proved very fruitful, namely, "What are the aquatic respiratory adaptations of terrestrial insects?" This led to the discovery that plastron respiration was more common among terrestrial than aquatic insects (Hinton 1960a) and it also focused attention on the phenomenon of submergence akinesis (Hinton 1976).

There is reason to believe that the common ancestor of the subphylum Antennata, like that of the Tardigrada and Chelicerata, lived in a saturated terrestrial environment in litter or just beneath the surface of the soil. They were originally small animals that in this environment could rely upon cutaneous respiration. But the chance of being exposed to desiccating conditions from time to time was always present and so there was always heavy selective pressure for the evolution of a tracheal system that would enable them to restrict to some extent humidity exchanges with the ambient air.

In fact, two classes related to the Insecta (far more so than the Collembola that are usually placed in the Insecta) are the hexapod Diplura and the myriapod Symphyla, both of which have a tracheal system and a more or less permeable bodywall cuticle and live in damp litter or beneath the surface of the soil. Perhaps the ancestral Antennata could tolerate more or less total dehydration and to begin with solve the problem of desiccating conditions in this way, as, for instance, tardigrades still do.

Some of you may be astonished at my mention of the Chelicerata as primitively terrestrial in view of the extensive review by Tiegs and Manton (1958) but in this review, as in Manton's later work, the assumption is made that *Limulus* is a primitive chelicerate. However, some of the terrestrial chelicerates, such as the Palpigrada and Solifugida with a segmented prosoma, combine in themselves many more primitive chelicerate features than the Merostomata, as shown by Versluys and Demoll (1922).

Early in their evolutionary history insects evolved a form of body upon which, so to speak, an endless number of variations could be made without materially altering the basic plan. Insects, more than the members of any other large group of invertebrates, always look like insects with really very few exceptions, as, for instance, the females of some Strepsiptera. The members of no other large group of invertebrates are so easily recognizable for what they are. Certainly not the Chelicerata, and even the Crustacea with fewer species than the beetles of the family Carabidae include more basically dissimilar things than all insects together. This difference is also striking when insects are compared with some other groups of invertebrates, e.g., among molluscs the difference between a slug and an octopus (with an eye as complicated as the vertebrate eye) is far beyond that found between one insect and another.

Contradictory Demands of Respiration and Water Conservation

The success of insects has been achieved on land, and, furthermore, in terrestrial environments that are not saturated or at least not saturated most of the time. It has been achieved in environments that other small animals have been unable to colonize simply because they were unable to solve the problem of exposing an area of body sufficiently extensive enough to satisfy their oxygen requirements without losing too much water to the ambient environment.

For organisms that require oxygen, it would have been much simpler to evolve a membrane that was at once permeable to oxygen and impermeable to water. But in some three thousand million years no such membrane has been evolved. The reason for this is simple enough: the oxygen molecule is appreciably larger than the water molecule. Thus any membrane with holes large enough to allow oxygen to pass will also allow water to pass. Respiratory membranes tend to be wet because water is being lost through them and not because the film of water on them assists respiration in any way. On the contrary, the film of moisture greatly slows down the rate of diffusion inwards of oxygen. A frog's skin is moist because the frog is losing water through it and not because it needs a moist skin in order to breathe. In fact, the occupation of dry terrestrial environments is impossible for the frog because it loses too much water through its skin.

Because of the difference in the size of the oxygen and water molecules, an environment with less moisture than the tissues of the animal presents it with incompatible demands: on the one hand it must have an extensive surface through which to take up oxygen, but, on the other hand, it cannot afford to lose water through an extensive surface. These incompatible demands of terrestrial environments have been partially resolved in different ways by all terrestrial animals. Most vertebrates are entirely dependent upon being able to replenish at frequent intervals the water lost through respiration, others rely heavily upon the combustion of fats to tide them over short periods of water shortage, whereas still others, i.e., some desert rodents, are able to metabolize all of their water requirements.

Insects and some Arachnida are the only arthropods that have dealt successfully with the incompatible demands of dry environments. The exposed cuticle is water-proofed, and effectively oxygen-proofed, usually by a continuous fatty acid layer. At the same time, an enormous surface area freely permeable to both oxygen and water is invaginated and forms tracheae that ramify through the body. The air in the tracheae can be kept saturated and the loss of water can be reduced to manageable proportions because the total surface area of the spiracles is only a very small fraction of the total surface area of the tracheae. As a further improvement, most insects have an apparatus that can close the spiracles and so prevent water loss through them when they are not actively taking in or expelling gasses. A few insects, e.g., some scarabaeid larvae and all dipterous larvae without exception,

have secondarily lost the closing apparatus of the spiracles. In these forms the spiracular atrium has numerous fine microtrichia that by pressure resistance and frictional drag reduce the loss of water. In some dipterous larvae and a few others, the cuticular microtrichia of the spiracular atrium are very dense and form a felt-like matting that more or less restricts movements of gas through the spiracles to diffusion.

It is of interest to note how acellular and primitive multicellular organisms, e.g., algae and some rotifers, nematodes, and tardigrades deal with the contradictory demands presented to them by environments that from time to time become drier than their tissues. These organisms simply dry up and are able to tolerate prolonged periods of dehydration when their metabolism is reversibly at a standstill. That is, they enter a state of cryptobiosis. Many insects that are irreversibly injured when their moisture content falls about 20% or so, nevertheless have tissues, e.g., epidermis (Hinton 1957) and blood cells (Selman 1960), that tolerate total dehydration and suspension of metabolism. So far, however, only one insect is well known that in the larval stage can tolerate dehydration and suspension of metabolism for years at a time, and that is the larva of the African chironomid midge, *Polypedilum vanderplankei* Hinton. It is important to note that although some of the tissues of this larva may have retained the primitive capacity to tolerate dehydration, the capacity of the whole larva of *Polypedilum* to tolerate dehydration is *secondarily* evolved and is not primitive.

Other species of *Polypedilum* are like ordinary insects: they cannot tolerate much dehydration. If even within a single genus there can be forms that tolerate any amount of dehydration and those that do not, we might well ask why have not more insects evolved a tolerance to dehydration of the kind evolved by *Polypedilum*. I think that the simple answer to this question is that to evolve this method of dealing with the incompatible demands of alternately wet and dry environments means that during dry periods the animal is in a state of suspended animation and so long as it is dry it cannot exploit the environment in any way. In the very especial environment in which *Polypedilum* is found there is a selective advantage in being able to dry up and enter a state of cryptobiosis. But for the organism to dry up means that for long periods of time it cannot exploit its environment, which is a great selective disadvantage suffered by acellular organisms simply because they have not the mass of tissue necessary to do anything about it. Furthermore, when dry and in a state of cryptobiosis any mechanical or other injuries are not repaired but accumulate so that when hydrated a summation of these minor injuries may be quickly lethal. If I may digress slightly, the selective value of the tough coats of the resistance spores of acellular organisms probably lies chiefly in preventing mechanical damage, which, as I have said, summates when they are dry and in a state of cryptobiosis.

Before passing on to other matters, let us consider for a moment the chief attributes of *Polypedilum*, attributes that, as noted before, are common to some tissues, e.g., the epidermis, of many insects. Figure 1 shows a dry larva of *Polypedilum*, and the same larva 3 years and 3 months later, 20 minutes after it was placed in water. As the larva became hydrated, a portion of the gut was forced through a tear in the cuticle made at the time the larva was dug out of the dry mud. This injured larva died about 4 hours after it was placed in water. Thus, the effects of an injury that was to be lethal in about 4 hours were postponed for 3 years and 3 months because the larva was dry and in

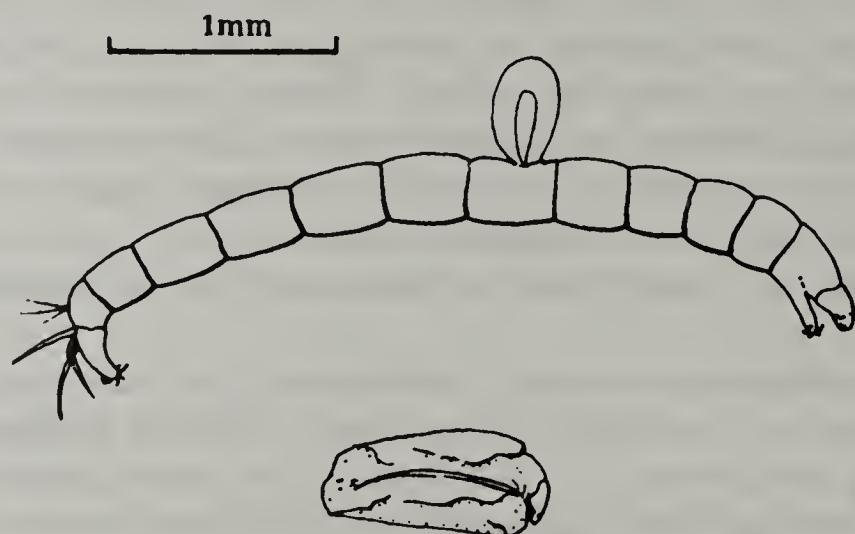


Fig. 1. —*Polypedilum vanderplankei* Hinton. Larva dried for three years and three months and the same larva 20 minutes after immersion in water. This particular larva had the tergite of the third abdominal segment torn open during the years that it was dry. A section of the gut was forced through the tear when it absorbed water, and the larva ceased to move about and died about 4 hours after it was placed in water (after Hinton).

a state of cryptobiosis. During cryptobiosis when metabolic activity comes reversibly to a standstill, the animal is a morphological and not a physiological entity. We could say that the larva has to be brought around before lethal injuries can have their effect. Experiments with *Polypedilum* clearly show that a distinction must be made between biological and calendar age. The biological age of two larvae may be exactly the same, say, 3 weeks, whereas the calendar age of one is 3 weeks and that of the other 4 years and 3 weeks if it has been in cryptobiosis for 4 years. Although in my experiments the calendar age of one larva was sometimes as much as 70 times that of another, there appeared to be no differences between them in activity or subsequent developmental history. In a state of cryptobiosis (even when the moisture content of the tissues is as high as about 7%) the larva can be immersed directly into liquid gasses, including helium, without injury. When the larvae are thoroughly dried they may be heated to just over 100°C . For instance, of 30 larvae heated to $102\text{--}104^{\circ}\text{C}$ for one minute, all recovered and 3 subsequently metamorphosed. It has also been shown that when in cryptobiosis the larva will metamorphose after immersion for 24 hours in 100% ethanol or for one week in pure glycerol (Hinton 1960b, 1968, 1971).



Fig. 2. —Larva of *Polypedilum vanderplanki* Hinton of continuous dehydration. Photograph with polaroids not crossed to extinction.

Conserving water by having an impermeable cuticle has imposed strict limits on insects in other directions. They can no longer cool themselves effectively because the bodywall is impermeable, quite apart from the cost in water that this would involve when they are in places where they cannot drink. Flushing air through the tracheae is, apart from seeking the shade, the only method of cooling open to them, but again this method is very expensive in terms of water. The fact that insects are not able to sacrifice water for cooling over long periods means that in warm climates insects run a real danger of overheating. An insect the size of a bumblebee or locust during flying may raise its body temperature as much as 15°C above that of the air. Thus when ambient temperatures are high, they can only fly a limited time if they are not to reach a critically high temperature. Although as individuals insects are poikilotherms, social insects may, as groups, be homiotherms. Honeybees maintain a nest temperature of about 36°C over a wide range of ambient temperatures. Even at -40°C

the nest temperature only falls to about 30°C. Thus, by adjusting the size of the cluster to restrict loss of heat, groups of bees tolerate long periods at ambient temperatures that are immediately fatal to a single bee.

It is often said that their method of respiration puts a strict limit on the maximum size attainable by insects because diffusion is not an efficient way of gas transfer when distances begin greatly to exceed the mean free path of gas molecules. But we only have to watch an insect move, especially a soft-bodied one, to see that tidal flows of air must be generated in the main tracheae. There is no reason why an insect should not grow to any size by simply having enough tracheal trunks so that a tidal flow of air is brought to within a few microns of any tissue. Nevertheless, their mode of respiration is one factor that sets a limit to the maximum size they can obtain but not so much because of diffusion problems but simply because as they grow larger they are involved in more and more massive gas exchanges with the ambient air, which in turn involves them in an increasingly intolerable loss of water.

The rigidity of the bodywall cuticle is often given undue weight as a factor in the success of insects. Most insects have a soft and pliable bodywall cuticle, and a high proportion of the muscles operate against turgor pressure. The insects with the most rigid bodywall cuticle are beetles, but most beetles are larvae and in most beetle larvae the cuticle is not rigid but is soft and pliable: most muscle action is against turgor pressure and not other muscles. In some insects, e.g., larvae of ceratopogonid flies, I have found that the only muscles in the whole of the body that do not operate against turgor pressure are those of the head. Still another common tale is that insects do not have an internal skeleton, but in the head of most larval and adult insects the bodywall has been invaginated to form a complex skeleton called the tentorium. Some years ago I showed (Hinton 1963c) that at ecdysis the tentorium splits along preformed lines of weakness just as does the bodywall cuticle. Perhaps an equally elaborate skeleton is not formed in the thorax and abdomen simply because, unlike the head, many muscles operate against turgor pressure. The importance of the pressure of the body fluids in locomotion and other movements decreases as the rigidity of the bodywall increases (Hinton 1955). Of course some insects, especially some adult beetles, have a very rigid exoskeleton, but even in these some muscles operate against turgor pressure. For instance, levation of the claws is by turgor pressure: the whole of the subphylum to which insects belong, the Antennata, lack levator muscles of the claws present in the Chelicerata and Crustacea.

Insects with semi-rigid or rigid exoskeletons solve another problem in a very neat way. The F_1 adult of a hard and rigid beetle begins life with the same displacement as the parents but its mass is much less. The problem of allowing an increase of mass within the same rigid container is solved by having tracheal airsacs. In certain silphid beetles of the genus *Speonomus* that live in caves (e.g., *S. longicornis* Saulcy) the larvae neither eat nor drink before pupation and yet produce an adult of the same size as the parents (Deleurance-Glason 1963). Here clearly much of the space in the young adult must be occupied by airsacs that are gradually flattened as its mass increases with feeding. In some female insects part of the space later to be occupied by the ripening eggs is provided by airsacs, e.g., the locust. Thus, the chief selective value of airsacs in adult insects is not in providing air stores but in allowing growth of tissues within a more or less rigid framework (Clarke 1957).

Origin of Wings and the Revival of a Bizarre Theory

One of the major reasons for the success of insects is, as Snodgrass once said, that they are the only group of animals that has evolved wings without the loss of a pair of limbs. I do not think that there can be any doubt that wings were evolved from lateral outgrowths of the thorax that functioned to increase the glide distance, as first suggested by Fritz Müller (1873). But there is an even earlier step in the evolution of wings, which I have called 'attitude control in falling' so that the insect landed in a position from which it could make a quick escape from predators (Hinton 1963b, Fowler 1964). The third step or nodal point in the evolution of wings was sustained flight by flapping the outgrowths previously used for attitude control and gliding.

In passing, it may be mentioned that Wigglesworth (1973, 1976) has recently revived the idea, perhaps first suggested by Oken (1811), that wings were evolved from gills. Wigglesworth has added his own peculiar twist to this theory and says (1973, p. 128) that, "... the thoracic styli of the Apterygota were the precursors of insect wings" In developing this bizarre theory, Wigglesworth explicitly says that the styli of the Thysanura are all that remains of the exopodite of a primitive insect appendage, which he considers to be biramous. I think that the days when entomologists were

persuaded by comparative morphologists, who were themselves cowed by specialists on Crustacea, into thinking that the primitive insect appendage was biramous are now gone, apart from the fact that the styli of the Thysanura are secondary adaptive organs that in some primitive members of the order (Machilidae) do not appear until after the third apolysis.

Metamorphosis and Success

The relationship between the structure of hormones and the changes that occur during metamorphosis is purely conventional in the sense that no amount of knowledge about the structure of hormones can tell us anything about the nature of the metamorphoses they trigger. We now know that chemically identical hormones will trigger the changes that occur during the metamorphosis of, say a cockroach, and the very different changes that occur during the metamorphosis of a beetle or butterfly. A simple analogy will dispel any doubt about what I mean. The red of a male stickleback during the breeding season elicits a behaviour pattern in other sticklebacks that has nothing whatever to do with the physical nature of red: no amount of investigation of the wave lengths that are interpreted by us as red will provide any clue to the behaviour pattern that red may elicit in this or that animal. Although the relationship between the structure of the hormones and the changes that occur at metamorphosis is conventional in the sense that I have indicated, it is not to be denied that a sufficient knowledge of the structure of a hormone may help us to determine the probable structure of the next step in the causal chain.

Many endocrinologists imply, when they are not actually explicit about the matter, that they were led to be endocrinologists first and foremost because they wished to contribute to an understanding of the significance of metamorphosis. The fact that chemically identical hormones can trigger the change from a larval *Rhodnius* to an adult *Rhodnius* or from a larval fly to a pupa and then to an adult is, I think, ample evidence that the nature of the hormones concerned has nothing whatever to do with the form or structure of the changes produced. Or to put the matter in a more general way, investigations into hormones that trigger metamorphosis has told us nothing whatever about the manner and conditions under which insects have evolved quite different kinds of metamorphoses. And it is some of these kinds of metamorphosis that have enabled insects to become so successful.

The success of a group of animals is here judged by the number of species that it has. A more realistic judgement would be based upon its capacity to control the environment, and a single species, man, does this beyond the scope of all others together. About 88 percent of known species of insects are endopterygotes. Whatever view we may take about the proportion of the total number of species described, it seems reasonable to suppose that the proportion of endopterygotes to exopterygotes will not be greatly altered by new discoveries. In discussing the success of insects it is therefore essential to understand why the endopterygotes are so much more numerous than the exopterygotes.

In the following discussion I use the terms exo- and endopterygote instead of the misleading terms hemi- and holometabolous. Many of the tissues of endopterygotes develop in a typically hemimetabolous manner, e.g., the indirect flight muscles of many Diptera-Nematocera (Hinton, 1959). It is only in the most specialized endopterygotes that there is a complete transformation of most of the tissues. However, in all exopterygotes the metamorphosis of the midgut differs in no particular way from that of the vast majority of endopterygotes. Many individual tissues of exopterygotes undergo a complete transformation: e.g., the labial mask of dragonfly larvae. Mäkel (1942) has shown that no less than 10 percent of the 200 skeletal muscles of male *Pseudococcus* are from myoblasts in the larval muscle-fibre syncytium or from scattered myoblasts. In a very large number of exopterygotes it is only necessary to glance at the last larval instar and adult to see that an enormous amount of remodelling of the epidermis must occur at metamorphosis (e.g., Fig. 3), an amount of epidermal remodelling hardly less than that of many endopterygotes. It seems to me that if the terms hemi- and holometabolous are to be used at all, they should be applied only to specified tissues and not to whole insects that are mixtures of tissues that metamorphose quite differently.

Anderson (1972a, b) published two extensive reviews on the developmental systems of insects. These are well-illustrated, and there are references in plenty. The casual reader might therefore overlook the basically anti-selectionist views of this writer, who revives some ancient and obscurantist views about the metamorphosis of insects, views that one had hoped were now only of concern to historians. Briefly, he gives full support to the Berlese-Imms idea that the differences between the metamorphosis of the exopterygotes and endopterygotes is entirely determined by the amount of

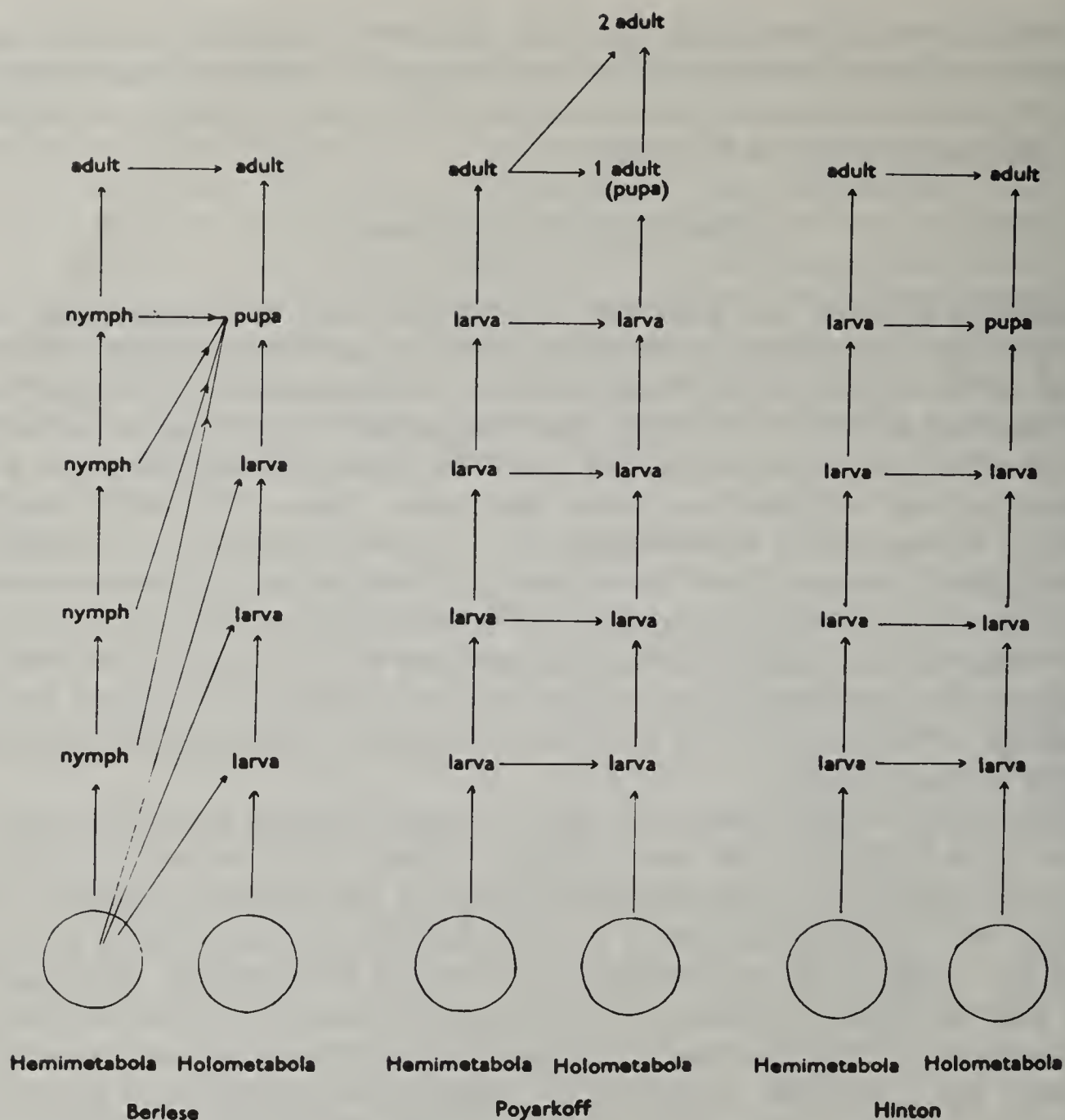


Fig. 4. —Diagram showing the relationship between the theories of Berlese, Poyarkoff, and Hinton (after Hinton).

the forms of the chief kinds of larvae are determined by the times of hatching. They claim that the larvae of the exopterygotes, which they call nymphs, have hatched, because of the greater amount of yolk in the egg, in a post-oligopod phase, whereas the larvae of sawflies, Mecoptera, and Lepidoptera have emerged from the egg in a polypod phase because they have less yolk in the egg. The apodous larvae of the endopterygotes are regarded by them as derived from the oligopod phase by reduction and loss of thoracic appendages. The theory of Berlese postulates two primary categories of larvae: the oligopod or pre-oligopod and the post-oligopod (nymph).

Berlese and his followers claim that it is the relative amount of yolk in the egg that determines the embryonic phase in which the larva hatches. This and similar theories explicitly state that the abdominal prolegs of endopterygote larvae are serially homologous to thoracic legs, a view already rejected by Deegner (1909) and many others. Prolegs are secondary adaptive organs that have evolved time and again in the endopterygotes (review in Hinton 1955), and some have more than one pair of prolegs on a single metamere (Fig. 5). In the Diptera alone, prolegs have been independently evolved at least 27 times (Hinton 1955).

Anderson (1972a, b), like Berlese and the modern adherents of his theory, maintains that the eggs of the endopterygotes are smaller than those of the exopterygotes and ignores the many who have pointed out that this is not so, e.g., Miall (1895), Hinton (1955, 1963a), and others. Anderson (1972a, p. 100; 1972b, p. 167) provides two tables of the dimensions of the eggs, one of exopterygotes and the other of endopterygotes. One would have thought that the veriest amateur would have taken into account the size of the female on the principle that large animals tend to lay larger eggs than small ones. In his tables the largest endopterygote is the passalid beetle, *Popilus disjunctus* Ill., whereas his list of exopterygotes includes some very large insects such as large mantids, stick insects, and *Locusta*. A realistic comparison would be to compare the ratio of the dry weight of the females to that of their eggs. In the absence of sufficient figures of this kind, the major axis of the egg as a percentage of the length of the body of the female of 102 species of exo- and endopterygotes is shown in Table 1. Differences in shapes of females and eggs are of course very important, but to

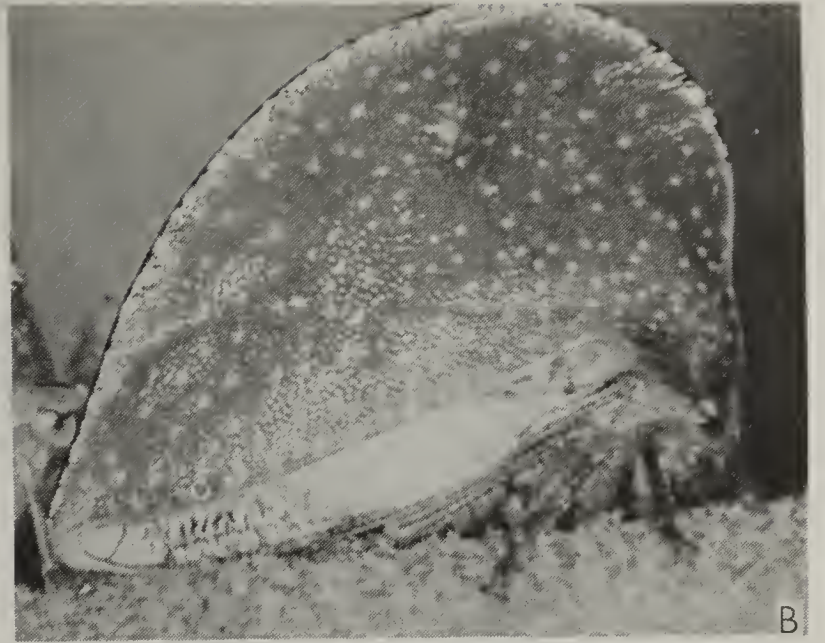


Fig. 3. —The membracid bug, *Antianthe expansa* Fowler. (A) Final instar larva. (B) Adult. The amount of metamorphosis undergone by the epidermis at the larval-adult apolysis is clearly comparable to that of most endopterygotes.

yolk present in the egg. As we have seen, only about 12% of all insects are exopterygotes. A corollary of what people like Anderson are saying is that the lack of success of this group, as compared with endopterygotes, is that they have more yolk in the egg. What is implied is that the amount of yolk in the egg is somehow or other fixed and not subject to selection. Anderson naturally feels called upon to provide tables of figures to support his arguments, and we shall see in a moment just how absurd these are.

But first let us see this whole matter in historical perspective. As early as 1651 William Harvey said that it was the lack of food reserves in insect eggs that caused what he called their premature birth. In an interesting paper on this subject Wigglesworth (1966) supports the views of Swammerdam and notes that only 18 years after Harvey made his statement, Swammerdam (1669) in his "*Biblia Naturae*" points out that the eggs of higher insects such as beetles, butterflies, and bees are not notably more deficient in yolk than those of *Lepisma* or grasshoppers. Swammerdam excused the mistake of Harvey on the grounds that insects are difficult to study "unless by persons accustomed to experiments of this kind; it is no wonder that the most happy geniuses, the immortal Harvey, for example, and many others should have fallen into error."

The Berlese theory might be described as an elaboration of the thesis of Lubbock (1874, p. 80), "That the occurrence of metamorphosis arises from the immaturity of the condition in which some animals quit the eggs." It is instructive to see how the adherents of Berlese's (1913) theory explain the differences in the development of the exo- and endopterygotes. For instance, Imms (1937, p. 36) says. "... the pupa along with the antecedent prepupa, are the ontogenetic counterparts of the nymphal instars of the lower orders of insects. It seems that tachygenesis, or shortening of development, has resulted to the extent that the whole series of nymphal instars has become concentrated into these two stages, with the elimination of the intervening ecdyses." The larvae of exopterygotes were called nymphs for no other reason than that people thought they were homologous with the pupa of the endopterygotes. And this homology, which to me seems absurd (Hinton 1963a), was well established in the minds of many long before the time of Berlese. It is common to find writers of the middle 19th century using the phrase "nymph or pupa" when referring to the larvae of exopterygotes. Some early writers, e.g., Burmeister (1832) and Westwood (1839), called the first instars of exopterygotes larvae and the later instars with obvious wing pads nymphs or pupae, and some recent German writers refer to the early larval instars of a cockroach as larvae and the later instars as nymphs. The three fundamentally different views about the relationships between the life-cycles of the exo- and endopterygotes are shown diagrammatically in Fig. 4 and have been discussed at length elsewhere (Hinton 1963a).

In a broad general way it is possible to distinguish three phases in the development of embryonic appendages. The appendages of the head appear first and are followed by the thoracic and a little later the abdominal. The appearance of the abdominal appendages marks the end of the protopod and the beginning of the polypod phase. The polypod phase passes into the oligopod when the metameric abdominal appendages are absorbed. According to Berlese (1913) and Imms (1937)

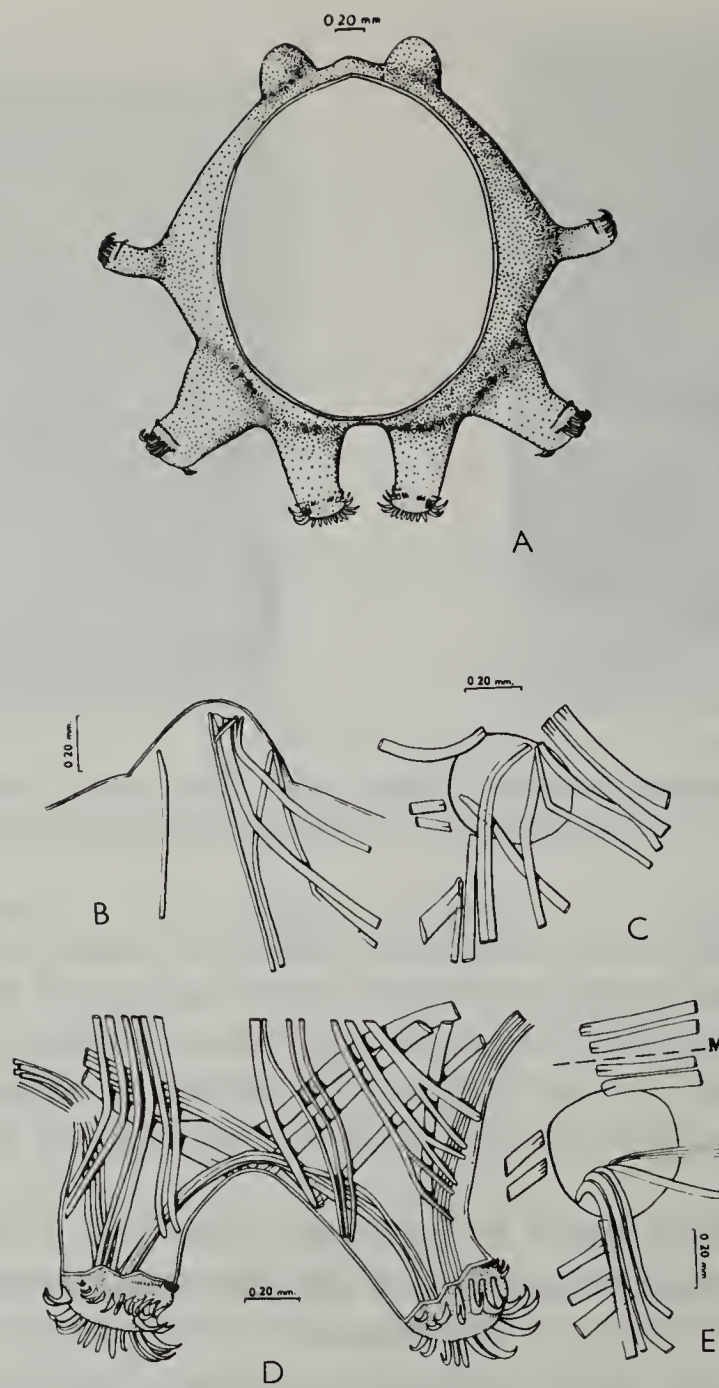


Fig. 5. —Larva of *Tabanus kingi* Austin. (A) Prolegs of third abdominal segment of mature larva. (B) Muscles of right dorsal proleg of 3rd abdominal segment. (C) Inner view from below of the right dorsal proleg of the 4th abdominal segment. (D) Muscles of ventral (left) and subventral (right) prolegs of 3rd abdominal segment. (E) Inner view from below of muscles of left dorsal proleg of 7th abdominal segment; (M) median line (after Hinton).

some extent such differences are “smoothed out” by the large numbers in Table 1. This table clearly shows that there is no distinction in size between the eggs of exo- and endopterygotes. The most obvious inference that can be drawn from Table 1 is that insects that lay thousands of eggs, like the Ephemeroptera and those Tachinidae with microtype eggs, have very small eggs in relation to the size of the female, whereas aphids and lathridiid and anisotomid beetles that lay few eggs have very large eggs in relation to the size of the female. Enormous differences in the size of the eggs can occur even within closely related groups. Among the Tachinidae the macrotype egg of *Gymnosoma* is about 2,000 times the volume of the microtype egg of *Zenilla*. Anderson (1972b, p. 169) devotes several lines to tell his readers how small coccinellid eggs are. But these beetles are small, and the fact is that their eggs are unusually large in relation to the size of the female. For instance, the length of the eggs as a percentage of the length of the body of the female is 33.3 in *Hyperaspis lateralis* Muls.

Anderson's concern with the size of the eggs is clearly because large eggs are supposed to have more reserves than small ones, but, as is clear from Table 1, neither the size of the egg nor its postulated reserves have anything to do with the differences between exo- and endopterygotes. In this connection it may be noted that in some endopterygotes much yolk is left between the embryo and shell after dorsal closure. For instance, the pharate first instar larva of *Lyctus* Spp. makes its first meal from the residual yolk-mass left in the anterior end of the shell (Alston 1923, Smith 1956). In many endopterygotes there is a cytoplasmic reticulum enmeshing the yolk and also often a distinct periplasm. However, in the Psocoptera, Pthiraptera, and Hemiptera there is also usually a distinct cytoplasmic reticulum and a thin but definite periplasm.

Perhaps it will now come as no surprise to the reader to find that Anderson attempts to shore up his argument by producing two tables (1972a, pp. 96; 1972b, 166) in which examples are chosen

Table 1.—Major axis of egg as a percentage of length of body of female from vertex of head to tip of abdomen. Exopterygotes are indicated by an arrow.

	Number of species	Mean	S.D.
Tachinidae (microtype)	3	1.35	1.31
⇒ Ephemeroptera	17	2.15	1.13
Tachinidae (macrotype)	5	8.66	1.89
⇒ Pentatomidae	5	11.30	1.48
Tenebrionidae	4	11.56	3.80
⇒ Acrididae	5	13.09	2.89
Staphylinidae	5	13.90	1.84
Aphelinidae	4	14.31	3.11
Dermestidae	10	16.84	5.25
⇒ Psocidae	6	20.50	5.79
⇒ Tettigoniidae	12	22.26	8.59
Muscidae	9	25.61	5.89
Lathridiidae	6	26.98	5.08
Anisotomidae	5	34.60	6.62
⇒ Aphididae	6	44.00	12.81

to show that exopterygotes develop more slowly than endopterygotes. One is surprised that the editor permitted the publication of tables purporting to compare speeds of development in which no indication whatever is given of relevant temperatures. Perhaps needless to add, in these tables Anderson has confused the embryo with the first instar larva before it has hatched.

The reasons for the great success of the endopterygotes as compared with the exopterygotes have already been discussed at some length (Hinton 1948, 1963a). In the line that gave rise to the modern endopterygotes, the last larval instar became specialized as a pupal stage. This permitted for the first time the complete dissociation in form and structure between the feeding and growing stages and the distributive and reproductive stage. Of particular importance was the internal development and great supression of the wings during larval growth. This feature alone requires a pupal stage. Because of the space occupied in the larval thorax by muscles and other organ systems, there is insufficient room for the wing anlage to develop to the size required for the wings to be effective even though allowing some growth after evagination. One moulting cycle only is required to evaginate the wings. During this cycle there is considerable growth of the epidermis of the wings, and large pupal wing-cases are formed. A second moulting cycle is then required during which the epidermis is freed from the pupal cuticle and the number of its cells increases greatly with the result that the definitive adult epidermis is much folded within the pupal cuticle before secretion of the adult cuticle is completed. In the larva (Fig. 6a) both the anlage of the wings and the imaginal muscles require relatively little space in the thorax. After the larval-pupal apolysis, however, the volume of both the wings and the imaginal muscles increase enormously. The indirect flight muscles are destined to occupy almost the entire space in the thorax (Fig. 6b), and there is simply no room in the thorax for both developing wings and adult muscles.

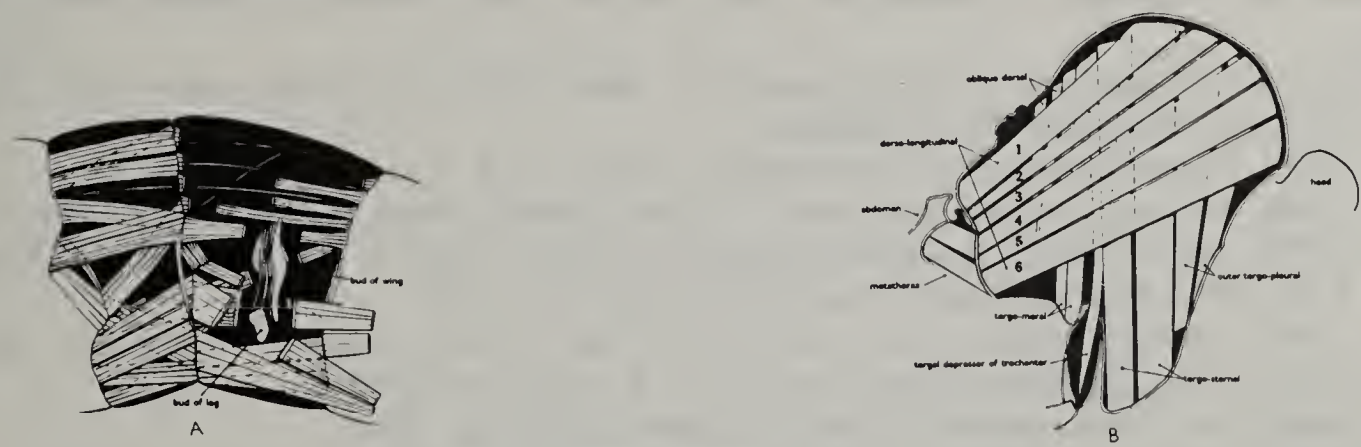


Fig. 6. —*Simulium ornatum* Meigen. (A) Meso- and metathorax of penultimate larval instar. The fibre rudiments of the trochanter are unshaded. (B) Meso- and metathorax of the adult.

The absence of external wings in the larval stages of endopterygotes enables them to burrow into solids — in the earth and in plant and animal tissues. It has, so to speak, pre-adapted endopterygote larvae to invade environments not available to larvae with external wings. Winged stages that burrow in the ground either shed their wings (like termites) or chew them off like ants. Cicadas are the outstanding exception among exopterygotes, and the very special adaptation that enables them to burrow and reverse in closely packed soil, their hinged wing-pads, has already been noted (Hinton 1948).

As we have noted in an earlier section, some of the tissues of many exopterygotes undergo extensive re-modelling of a holometabolous type. Some exopterygotes, e.g., Aleyrodidae, Thysanoptera, and male Coccoidea have one or two terminal quiescent larval instars in which there is a very extensive re-organization of tissues. Such modified larvae are similar to the pupa of an endopterygote in that they allow an extensive dissociation in structure between the growing and reproductive stages.

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Why Are There So Many Species of Insects?

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ABSTRACT

The number of species of insects is largely a function of how many species can coexist in a habitat (the "species-packing problem"). Species packing of insects involves the following concepts:

- 1) far more species of insects arrive at each habitat than can survive there,
- 2) most habitats are full,
- 3) insects are not a unique part of the trophic web,
- 4) extinction rates and immigration rates do not relate to species richness in a simple manner,
- 5) the direction and intensity of impact of habitat heterogeneity on species richness depends on the absolute amount of heterogeneity and on the productivity of the site,
- 6) the direction and intensity of impact of harvestable productivity on species richness depends on the heterogeneity of the site,
- 7) habitat heterogeneity and harvestable productivity are definable only in the context of the organism,
- 8) insects indirectly compete with each other through the contemporary and evolutionary medium of their host (prey),
- 9) as organisms get smaller, down to about insect-mite size, their ability to control their habitat declines, and
- 10) as organisms get smaller, down to about insect-mite size, the habitat heterogeneity increases.

A few applications of these premises are discussed.

This is a systematics symposium. Systematists have a chronic and expected interest in the reason why there are so annoyingly many species of insects. I am here because insect systematists reason that an ecologist should have something to offer on the subject. By asking someone like me to address you today, some systematist has thus implicitly recognized that the large number of species of insects is not the simple outcome of some inexorable speciation process that daily regurgitates more species onto the world. Rather, understanding why there are a certain number of species of insects is largely a species-packing problem. That is, what processes influence the numbers of species that can coexist in a given habitat, and what changes in the habitat would result in more or fewer species coexisting?

The species-packing problem is one that has fascinated a number of different kinds of biologists (e.g., Abele 1976, Brown and Lieberman 1973, Colwell 1973, Colwell and Fuentes 1975, Elton 1973, Heck 1976, Hutchinson 1959, Janzen 1968, 1970, 1973a, b, c, Johnson and Hubbell 1975, Kethley and Johnston 1975, MacArthur 1957, MacArthur and Wilson 1967, May 1973, McClure and Price 1975, Paine 1966, Peet 1974, Price 1971, Pulliam and Brand 1975, Rothke 1976, Simberloff 1970, 1974, 1976, Southwood 1960, 1961, Strong and Levin 1975, Titman 1976) and my goal here is not to explicitly review their work. Rather, I wish to set down some of the traditions of species-packing thought and apply them briefly to a few cases familiar to me.

In my opinion there are a small set of natural historical operating premises that are central to understanding species-packing. I will list them below and discuss each very briefly. Before I begin, one word, “habitat,” needs clarification. As used here, a habitat is any arbitrarily defined physical area with organisms, other resources and physical conditions present. Thus a habitat may be a rotting carcass, all rotting carcasses in a square kilometer, or all rotting carcasses. It may be a hectare of land centered on this rock. It may be an individual oak tree, all oaks of that species in a hectare, all oaks of that species on ridge tops, or all oaks of that species. It may be a stage in succession in a particular kind of forest, or just in general. It is large enough to contain one or more breeding populations of organisms at the time of discussion. There is one major gray zone in this characterization of “habitat.” The number of species present in a habitat is obviously one of its traits; however, this means that each time a species is added or eliminated (without deletion or replacement), the habitat has changed. Strictly speaking, I therefore cannot ask how the number of insect species in a habitat changes if, for example, I replace evergreen tree species with deciduous ones. However, pragmatically, there is no problem because, for example in this case, it is clear that the habitat has not been defined by the number of species of insects present, but rather by a trait of trees.

The term “species richness” means simply the number of species present (as opposed to “species diversity” which has a number of quite different meanings).

Some Operating Premises

1. Species Availability

In any given contemporary habitat, far more species of insects may be found on occasion than maintain a breeding population there. The larger the habitat, the less true this statement, with the entire earth as habitat as the limiting case. These transient species are available for colonization of that habitat. A major part of “why are there not more species in a habitat” is “why don’t these transients establish themselves?” *The most important implication of their presence is that the number of species in a contemporary habitat has little or nothing to do with speciation rates there or elsewhere.*

For convenience, the transients can be divided into approximately three kinds:

(a) There are waifs that are there because they happen to be passing through of their own or something else’s volition. Virtually all colonists of oceanic islands are in this category. The adaptive value of the traits that got them to the island is not the act of arriving at the island.

(b) There are regular visitors that obtain some part of their resources from the habitat in mind, but the habitat in which they are resident is some larger unit that contains the habitat in mind. Many species of solitary bees are in this category if the habitat in mind is a field of flowers.

(c) There are species that no longer occupy the habitat but once did; such species are transient in time rather than space. We will never know how many species of insects have, for example, occupied the habitat called “feeding on all members of the genus *Quercus*.” It is undoubtedly enormous and much larger than the number of species to be found in this habitat at any one time.

Transient species are often viewed as incidental to the species composition of a habitat, but this perception is clearly born of frustration with their large numbers rather than biological reality. There are a large number of poorly understood processes determining the number of transients in a habitat – proximity of other habitats, pattern of resource production in the habitat, species richness of other proximal habitats, longevity of the habitat in geological time, species richness of residents in the habitat, lethality of the habitat to transients, etc. These processes cannot be swept under the rug and we cannot forget that transients may constitute a major part of the prey input to a habitat (e.g., insects falling into forest streams) and consume a major part of the harvestable resources (e.g., stingless bees on flowers in forest treefall habitats). I know of no study that attempts to characterize the transient insects in a habitat *vis à vis* the residents.

2. Full Habitats

With one widespread exception, habitats are much closer to being full of species than empty. In other words, *all logical and pragmatic evidence suggests that the number of insect species in a habitat is very unlikely to change much over time unless the habitat is modified.* (Fig. 1) The widespread exception is that habitat which is defined as a species that has newly immigrated to a site that does

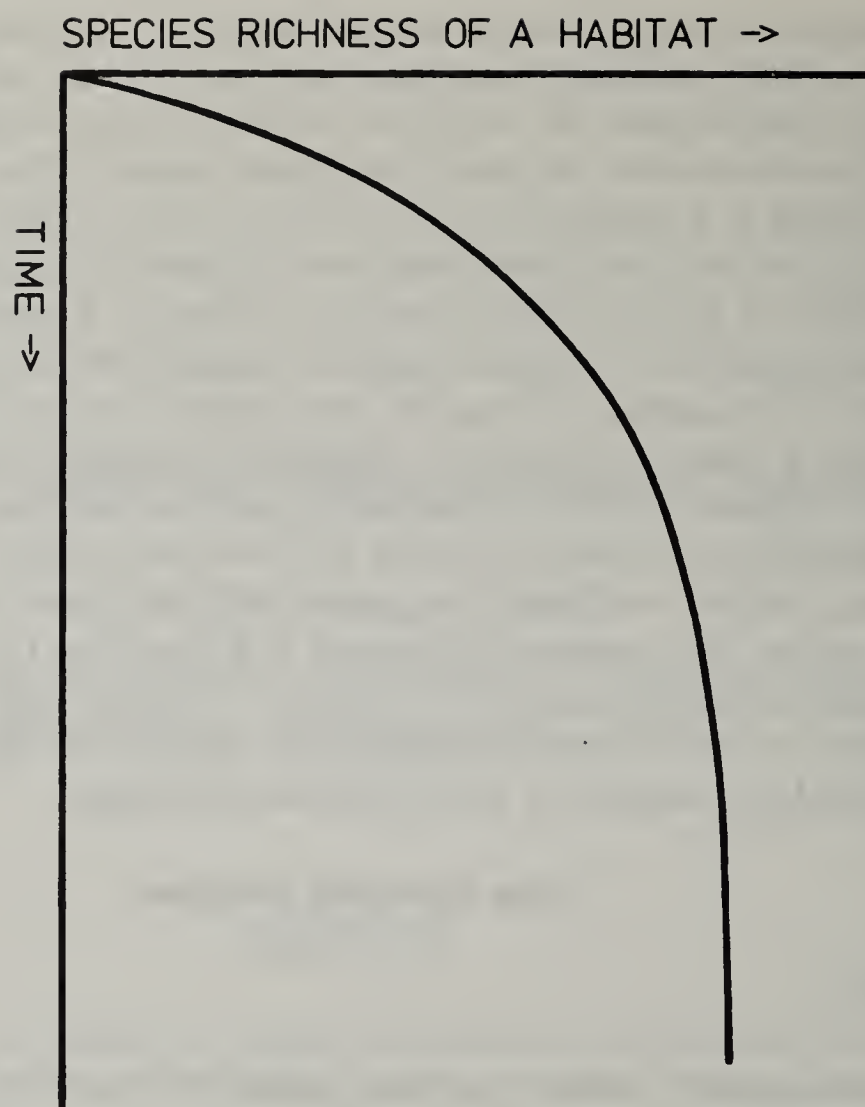


Fig. 1. –Hypothetical change in species richness of a habitat over geological and/or evolutionary time.

not regularly experience such immigration (e.g., a plant species moving from Africa to South America). In immigrating, it has left many of its residents behind. It will acquire a new set, the magnitude of which will be determined by its surroundings as well as its personal traits. I should emphasize, as Strong and his associates have recently stressed (Strong 1974a, b, c, Moore 1974, Strong et al 1976), that the initial filling of the new habitat with insect species may be very rapid. The speed will depend on the proximity, species-richness, and similarity of source habitats.

3. *Insects Non-unique*

Insect species richness per habitat cannot be examined in vacuo, since insects do not occupy a unique and separate portion of the trophic and productivity web. On the other hand, insects are not freely interchangeable with other consumers within or between habitats (or within or between places in trophic and consumer webs). The implication of this observation is that, for example, a compendium of the number of species of herbivorous insects that feed on a particular plant species may be very close to very far from a list of the herbivore load of that plant species. Or again, when considering the species richness of predaceous insects in a habitat, the species richness of insectivorous birds, toads, spiders, etc. has to be considered as well. In short, *there is probably not too much ecological meaning to a species list of insects for most habitats*; it may be satisfying to a taxonomist as a measure of the job left to do, but an army ant colony is ecologically no more similar to a leaf-eating melolonthine scarab than is an anteater. In the same vein, there is no hint that the ecological rules that apply to insects are any different from those that apply to other organisms.

4. *Extinction Rates*

As the extinction rate (loss of species per species per unit time) gets high, the rate of immigration of species to that habitat begins to influence the numbers of species present in the habitat at equilibrium. The implication of this generalization is that *in habitats with large numbers of species or low extinction rates* (e.g., tropical rainforest and adjacent swamps on mainlands), *the immigration rate may fluctuate widely without influencing the number of resident species present*.

A terminological note of caution is due here. I use “immigration” in its English language meaning – to arrive in a previously unoccupied habitat with no implication as to the eventual fate of

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Valerie Wright	USA
Donald P. Wright, Jr.	USA
William H. Wymer.....	USA
Rene Wyniger	Switzerland
M. Wysoki	Israel
Mariann Wyss-Huber	Switzerland
Shigemi Yagi	Japan
I. Yamamoto	Japan
Kageyuki Yamaoka	Japan
Keiko Yamashita	Japan
Tosiro Yasuda	Japan
Keizo Yasumatsu	Japan
Harry O. Yates III	USA
Wesley Eugene Yates.....	USA
Shoshana Yathom	Israel

David F. Yen.....	Taiwan	Takeshi Yushima.....	Japan
Lee Fong-Chen Yen	Taiwan	Al-Yafi Zafer.....	USA
William G. Yendol.....	USA	Dmytro Zajciw.....	Brazil
Scott R. Yocom.....	USA	*Lauren Green Zarate.....	USA
Wayne A. Yoder	USA	Nasser Zareh	USA
Masayoshi Yoshida	Japan	Thomas J. Zavortink.....	USA
Toshiharu Yoshida	Japan	Brian Zeichner	USA
Carl M. Yoshimoto	Canada	Ingeborg Zenner-Polania	Colombia
Chen-Wen Young	USA	J.L. Zettler	USA
David A. Young.....	USA	E. Zielke	Liberia
Mrs. David A. Young.....	USA	Mrs. E. Zielke	Liberia
G. Young.....	New Guinea	E. Zlotkin	Israel
Lester C. Young.....	USA	G.W. Zoebelin.....	W. Germany
Orrey P. Young.....	USA	Oscar C. Zoebisch	USA
Peter E. Young	USA	Eliezer Zomer.....	USA
William R. Young	Thailand	Robert Zwart.....	Netherlands
Mrs. William R. Young	Thailand	Gunter Zweig	USA
Ching G. Yu	USA	Peter Zwick.....	W. Germany

*Registered but not in attendance



Permanent Committee for the International Congresses of Entomology. *Seated*, left to right: Mound (Secretary Elect), Freeman (Secretary), Carvalho (Chairman), Ghilarov (Vice Chairman), Baccetti. *Standing*, left to right: Smith, Lindroth, Tischler, Yasumatsu, Waterhouse, Sabrosky, Pal, Landa, Hafez. Absent: Taylor.



Stage party at the opening session: The Permanent Committee (see above), plus Secretary-General Anastos (back row, left end), Dr. T. A. Taylor (back row, 3rd from left), Dr. H. J. McCracken (front row, 3rd from left; official welcome), and Dr. T. R. E. Southwood (front row, 4th from left; opening plenary speaker). The vacant chair is that of President Sabrosky, who was presiding at the podium.



President Curtis W. Sabrosky



Secretary-General George Anastos



T. R. E. Southwood, opening plenary speaker



Thomas R. Odhiambo, closing plenary speaker

Opening Plenary Session

(Led by President Sabrosky, the members of the Permanent Committee and Drs. McCracken and Anastos marched to their places on the platform. The meeting was opened with the national anthem, "The Star Spangled Banner," played by the Special Ceremonial Unit of the Navy Band, conducted by Chief Musician Art Accardo. The President thanked them for the music provided during the assembling period.)

Members of the Congress, Distinguished Guests, Ladies and Gentlemen:

For a formal welcome from this country, from our federal government, and from Washington, I introduce to you Dr. Ralph McCracken, Associate Administrator of the Agricultural Research Service of the U.S. Department of Agriculture. Dr. McCracken.

(Dr. McCracken)

Thank you, Dr. McCracken, for your words of welcome for this Congress.

The initiative for inviting the XV Congress to this country came from the Entomological Society of America. To represent the entomologists of the host country, I introduce to you Dr. Ray F. Smith, of the University of California at Berkeley, President of the Entomological Society of America. President Smith.

(Dr. Smith)

Thank you, President Smith, for your welcome from the Society and from American entomologists.

At this time, I wish to call upon Dr. George Anastos, Secretary-General of the Congress, for a few announcements that need to be made at this time. Dr. Anastos.

(Dr. Anastos)

Thank you, Mr. Secretary-General.

Introductions

(1) The Congresses of Entomology have a very few Honorary Members. Four are living, and one is here today. I am honored to introduce the distinguished insect physiologist from Cambridge University, England, Sir Vincent Wigglesworth.

(2) The Honorary Vice Presidents of the Congress are the president of the Entomological Society of America, and the presidents of the entomological societies of our good neighbors to the north and south — Canada and Mexico. The president of the Entomological Society of America has already been introduced. I am honored to present to you the President of the Entomological Society of Canada, Dr. George Cooper, and the President of the Sociedad Mexicana de Entomología, Dr. Jorge Gutierrez Samperio.

(3) The last previous entomological Congress in this country was held at Cornell University, Ithaca, New York, in 1928, nearly a half century ago, and the president of the Congress was one of America's world famous entomologists, Dr. L.O. Howard. I am pleased to introduce a member of that Congress and Dr. Howard's devoted companion, his daughter, Miss Lucy Howard. There are a few other members of this XV Congress who were also members of that IV Congress in 1928. Would those members stand and be acknowledged by the Congress? (The President recognized Louise Russell, Alan Stone, Floyd Smith, Dwight DeLong, Edson Hambleton, Frank Campbell, Mrs. R.E. Snodgrass.) We thank you for your enduring and steadfast interest in entomology and in the Congresses.

(4) I am sure that all Congresses would like to be innovative. I propose to make this Congress unique in at least one way: introduction of the Permanent Committee for International Congresses of Entomology. At the XIV Congress in Canberra, in 1972, my wife reported to me that someone near her asked "Who are all those people up there on the platform?" And I realized that although the Permanent Committee is always seated in a prominent place at the opening meeting, the members have never, in my memory, been introduced to a Congress. Therefore, may I introduce them now. Will each rise and be recognized as I call his name? Please — no applause for each individual; wait until

all are introduced and then we can applaud the Committee as a whole. (President Sabrosky introduced individually the members of the Permanent Committee.)

And now that I have given them their moment in the limelight, I propose to kick them off the stage. Will the Permanent Committee and Dr. McCracken and Dr. Anastos please move quickly to their reserved seats in the audience?

As they leave the platform, I may note that Dr. Waterhouse was President of the XIV Congress in Canberra in 1972; Dr. Ghilarov was Secretary-General of the XIII Congress in Moscow in 1968; and Dr. Freeman was Secretary-General of the XII Congress in London in 1964. So we can feel the hot breath of history as these gentlemen view the proceedings of this Congress.

It is not my intention to make a formal presidential address, but I do wish to make a few remarks at this time.

The International Congresses of Entomology have had a long and distinguished history. The first Congress was held in Brussels in 1910, and was attended by 250 members from 23 countries. The membership fee for that first Congress was the princely sum of 25 Belgian francs, or about \$5.00 at that time. Times have changed! That first Congress was so successful and enjoyable that another was arranged only two years later, at Oxford, England, in 1912. After a long gap during and after World War I, Congresses resumed with a 3-year interval; since 1956, a 4-year interval. The largest Congress was that at Moscow in 1968, with over 2,900 in attendance, and the second largest that at London in 1964, with over 1,800. Our Congress, in spite of the difficulties of inflation, austerity, budget problems, etc., in many parts of the world, will now be the second largest, with over 2,000 registered.

The 15 Congresses have been held in 13 different countries. England has hosted two Congresses, and this is our second. If I may be pardoned a personal item, this is my 8th Congress of Entomology, so I have attended over half of the 15 Entomology Congresses. My experience began with the VII Congress at Berlin in 1938, an experience that lives in pleasant memory. I would like very much to reminisce with memories of my seven previous Congresses, but time and demands of the XV Congress dictate otherwise.

No Congress has ever been perfect, and it is safe to say that none ever will be. I know that we have made some mistakes, despite good intentions and sincere efforts. We apologize humbly for these, and we beg your indulgence and your tolerance. Planning Congresses is difficult at best. Perhaps a Congress held in good times with a healthy world economy would not be subject to as many worries as we have had. However, even in the best of times, Congress planners need cooperation. I know that we have irritated some people by stringent requirements for pre-registration, dollar payments, housing, etc. But perhaps our experience and our methods will assist future Congresses in deciding what to do — perhaps what not to do.

The scientific program provides more time for symposia than for individual papers. It has long been recognized that the plethora of individual papers is one of the worst features of Congresses. At least one Congress in another field eliminated contributed papers altogether. This step seemed too drastic a break with the past for an entomological congress, but as an intermediate step we have emphasized carefully organized programs. Each morning is devoted to three major symposia, or a total of 15, one from each of the 13 Congress sections plus two others. For afternoons, sectional symposia and invited speakers are given major attention. We believe in this way a strong, solid program has been arranged.

We have tried a few so-called poster sessions, a recently developed means of handling a large number of contributed papers. Undoubtedly this is a new method for many of you. We hope that you will give this method a good try, or at least be interested in having the experience, for future reference.

I know that many entomologists are interested in postage stamps. We tried very hard to get a special insect stamp for the Congress but without success, chiefly because of the emphasis on historical subjects in this Bicentennial year of 1976. However, we believe that our efforts helped direct attention to the beauty and interest of insect stamps, and we understand that work is now going on for a set of 4 butterfly stamps to be issued in 1977.

Dr. Anastos has mentioned the President's Reception, and for the benefit of late comers, this is now scheduled for 7:00-9:00 o'clock this evening. Please be advised that you are not required to pass through a receiving line and shake my hand. You may do so, if you wish, *provided* that you do not hold my hand too long nor squeeze it too hard.

We hope that you enjoy our beautiful capital city of Washington. This is the Bicentennial Year for this country — our 200th anniversary as a nation. We are as a mere child compared with the

nations from which many of you come, but we are nevertheless proud of our 200 years of democracy. There are many special events and special exhibits in the city in connection with the Bicentennial. We hope that you find time to sample some of these and to visit our outstanding historical, cultural, and educational features.

Finally, for the Americans present, remember that this Congress is not hosted only by the officers of the Congress, or the Organizing Committee. Each of us is one of the hosts. May we all do our best to help make this a most memorable and pleasurable Congress for our fellow entomologists and their families from across the oceans and from other countries in the Western Hemisphere.

Our speaker at this opening plenary session is Professor T.R.E. Southwood, head of the Department of Zoology and Applied Entomology of the Imperial College of Science and Technology in London, England. His early work dealt with the taxonomy, morphology and biology of Hemiptera-Heteroptera and culminated in a large book, on the "Land and Water Bugs of the British Isles" by Southwood and Leston (1959). In the course of his biological work, he studied the immature stages, flight activity, mechanism of wing polymorphism, and insect-host relationships. So it was a natural move into studies of insect populations, sampling methods, etc., and he has become known in the last decade or so as an insect ecologist. I would cite particularly his 1966 book on "Ecological Methods with particular reference to the study of insect populations" and his editorship of the symposium on "Insect Abundance" (1968), a symposium of the Royal Entomological Society of London.

I am honored to introduce to you Professor Southwood, who will address you on the subject of "Entomology and Mankind."

Final Plenary Session

President Sabrosky: This is the final plenary session of the XV International Congress of Entomology. The speaker on this occasion is Professor Thomas R. Odhiambo, Professor at the University of Nairobi in Kenya, and Director of the ICIPE, the International Centre for Insect Physiology and Ecology, in Nairobi. Professor Odhiambo will address you on the subject "Entomology and the Problems of the Tropical World." Professor Odhiambo.

(Professor Odhiambo)

(President Sabrosky turned the meeting over to Chairman Carvalho of the Permanent Committee for the Congresses.)

President Sabrosky: Ladies and Gentlemen: We approach the final moments of the XV Congress. Will all those who helped with the Congress stand and be acknowledged? (Applause). We hope that you have enjoyed the Congress and have profited from the many meetings and the opportunities for personal contacts with friends old and new. There have been some sad happenings during the Congress. Our sympathies to families, friends, and colleagues. But life must go on, and does go on. Some of us will meet again, others will not. But for now, the officers and the entire staff of the XV Congress wish you all a safe trip home, and happy and productive days ahead in entomology. Thank you, and farewell!

Secretary-General Anastos has a few final announcements.

RESOLUTION AND ANNOUNCEMENTS SUBMITTED BY THE PERMANENT COMMITTEE

1. *Resolution from Section 1 on Scientific Collecting, Exchange and Transfer of Entomological Specimens*

WHEREAS, entomological specimens are indispensable material for the educational and scientific study of insects and other arthropods, and;

WHEREAS, entomological collections are permanent scientific resources, which are held in trust for use by the world scientific community, and;

WHEREAS, scientific collecting, exchange and transfer of entomological specimens is necessary in order to continue scientific inquiry and its rational application for the well-being of mankind, and;

WHEREAS, it is important that national and state regulations do not impede the appropriate use of scientific specimens in entomological research and education, and;

WHEREAS, the principle should be strongly endorsed that, where suitable museums exist for the safe long-term preservation of holotypes, these holotypes should be located in the region of the world where the species concerned occur, now

THEREFORE BE IT RESOLVED, that the XVth International Congress of Entomology, Washington, D.C., August 19-27, 1976 endorses the principle of exchange of scientific specimens of insects and other arthropods among scientists of all nations, and urges that when national and state regulations are made they be drawn in such a way that they are consistent with the foregoing preamble.

2. *Location of Next Congress*

An invitation to hold the next International Congress in Japan in 1980 was received from Dr. S. Masaki, President of the Entomological Society of Japan. The Committee recommended that this be accepted.

3. *Changes in the Composition of the Permanent Committee*

Dr. P. Freeman had expressed his wish to resign after 12 years of secretaryship and the Committee regretfully accepted his resignation. Resignations have also been received from Dr. G. Richard and Dr. C.H. Lindroth.

The Committee has been fortunate in being able to nominate Dr. L.A. Mound (United Kingdom) to replace Dr. Freeman both on the Committee and as Secretary.

The Committee also proposed that the following be appointed members of the Permanent Committee: —

Dr. E. Biliotti	(France)
Dr. S. Glumac	(Yugoslavia)
Dr. M. Hafez	(Egypt)
Dr. J. Keiding	(Denmark)
Dr. C.E. Machado-Allison	(Venezuela)

4. *Honorary Members of Congress*

The deaths were reported with regret of Professor J. Chester-Bradley and Dr. K. Holdhaus. It was proposed that Dr. C.H. Lindroth, a retiring Committee Member be appointed a new Honorary Member.

The foregoing resolution, recommendations and proposals, submitted by the Permanent Committee were approved by the Plenary Session of Congress.

IN REMEMBRANCE

POWERS S. MESSENGER.—It is with regret that we announce the death of Professor Powers S. Messenger, Chairman of the Department of Entomological Sciences, University of California, Berkeley, on Monday, August 16, 1976, in Berkeley. Born in Redding, California, August 14, 1920, Professor Messenger received both his Bachelor of Science Degree (1942) and his Ph.D. degree in Agricultural Chemistry (1951) at the University of California, Berkeley, and joined the University as an entomologist in 1951. In 1965 he was appointed professor of entomology. He was Chairman of the Department since 1973. His research included the influences of temperature on growth and reproduction of insects, the ecology and biological control of the Oriental fruit fly and the relationships between various other pest insect and parasite systems. Contributions in Dr. Messenger's memory may be made to the Powers S. Messenger Memorial Fund in care of the Department of Entomological Sciences, University of California, Berkeley 94720.

FATHER WALTER W. KEMPF, OFM.—Father Kempf, recently appointed Professor at the Department of Animal Biology, University of Brasilia, editor of the Brazilian

magazine *Studia Entomologica*, died suddenly of a massive coronary attack Friday, 20th August, at 2 AM at the Providence Hospital, after receiving all possible care from his Franciscan Order Brothers.

His body was sent to Brazil — Sao Paulo — according to the arrangement made between the two Provincial superiors.

He brought a paper to be presented at the Congress, "A Preliminary Zoogeographical Analysis of a Regional Ant Fauna in Latin America," and was finishing the memorial issue of the *Studia Entomologica* in honor of Father Thomas Borgmeier, the former editor, who died last year.

Entomology and Mankind

T.R.E. SOUTHWOOD

Department of Zoology & Applied Entomology, Imperial College, London

Entomology is a science that has some of its origins in both theology and art. Even today there is an aspect that might be said, from the skills demanded, to be an art and other facets that can fairly claim a place in the fine arts. The breadth of the subject contributes to its fascination. It is a hobby and also a profession; indeed for some it can be both without in any way restricting their intellectual experience. This plurality in the genesis of entomology may be seen in the dictionary definitions; whilst the Oxford and other British dictionaries generally describe it as 'that part of natural history that treats of insects,' French and American dictionaries tend to define it as a 'branch of zoology.' It is perhaps surprising that in 1745 the Swiss entomologist Charles Bonnet entitled his book "Traité d'insectologie" and expressed the view that "entomology" had a barbarous sound.

The many facets of entomology mean that it has impinged on mankind in multiple ways. There is firstly that corpus of science and art that strictly constitutes entomology and many persons have derived pleasure from it, just as they may from literature, art, or some useless but intellectually demanding branch of learning, heraldry or chess. The objects of this study, the insects, do however affect mankind as a whole: through both health and food supply. In many fields insects are man's greatest competitors and therefore though our subject is intellectually satisfying in its own right, it has to many, if not all of us, the added, perhaps overriding satisfaction of contributing to the alleviation of human suffering and the better management of the biosphere. The challenge of our subject is now greater and broader than ever. Having the great privilege of reviewing it before this Congress I intend to examine each of these aspects in turn: pleasure, welfare, and the management of the biosphere, co-existence.

Entomology's role in culture and recreation

In ancient Egypt the scarab beetle (*Scarabaeus sacer* L.) had an important place in religion and writing. The ball of dung it forms and rolls to provide an oviposition site was considered to represent the sun. Hence the scarab hieroglyph, pronounced 'Khopi' or 'Kleper,' represented the verb "to create" or "to become" and scarab images, both large and small, were widespread. The small seal images, that often had messages underneath such as 'Ammon protecteth' or 'Mut give thee long life', were particularly common in the New Kingdom (1580-1150 BC). The honey bee and fly were also represented by hieroglyphs (Harpaz 1973), but unlike the scarab these remained word pictures and did not become a phonetic symbol. There is a handsome representation of an aculeate, probably a bee, on the funerary bed of Queen Hetephras. Honey bees were widely depicted in the ancient world; this was generally associated with the function of providing honey and wax and will be discussed later.

Insects have also had an important role in lore and culture in other parts of the World, and I can only briefly allude to a few examples. The Praying Mantis has the major place in bushman mythology: the fact that the male dies during copulation (eaten by the female) emphasizes the cycle of death and rebirth, central to so many religions (van der Post 1961). Butterfly migrations involving at least 28 species (Williams 1958) are conspicuous in Sri Lanka and it was considered that these were pilgrimages to the sacred mountain, which is therefore called Samanala Kanda (Butterfly mountain). The honey bee has generally been extolled in lore, but with characteristic realism towards sexual

activities, in Indian literature it is compared with a lover, sipping nectar and moving on to a new loved one; in contrast the moth at a candle is like a lover who, unable to establish contact with his beloved (the candle) dies. Insects were sufficiently part of every day life in the sixth century BC for them to figure in Aesop's fables, whilst in the Mycenaean era the mythological Psyche was sometimes portrayed as a butterfly (Morge 1973).

Entomology, as we know it, had its slender beginnings in the writings of Aristotle, although the works of Chung Pzu show that the ancient Chinese philosophers also had some concept of metamorphosis (Needham 1956). After the collapse of the Roman Empire it was not until the Renaissance that entomology, like many other fields of human endeavour, again advanced. Initially the early encyclopaedic naturalists like Aldrovandi were as much scholars as observers and much reliance was placed on the works of classical authors: for example, Philemon Holland (1601) translated Pliny the Younger. However, Pliny and the medieval compilers had a strongly anthropocentric view of the Insecta, almost all the species discussed were those that impinged on health or food production, but the butterfly and firefly were included.

The first books entirely devoted to entomology were Aldrovandi's (1602) 'De Animalibus Insectis' and the multiple authored 'Theatrum Insectorum,' which contains contributions by Gesner, Wotton, Penny and was completed by Thomas Mouffet in about 1598. It was published in Latin in 1634 and an english translation in 1658. In the next hundred and fifty years the study of entomology made striking advances and publications ranged from Swammerdam's (1669, 1737) magnificent anatomical studies through Réamur's (1734-42) six volume memories to Moses Harris (1766) 'Aurelian' (Beier 1973, Tuxen 1973). Swammerdam and other invertebrate anatomists, such as Redi and Malpighi established the concept that insects were organized creatures with internal systems and life-cycles. Réamur emphasized the role of direct observation. The publication of Moses Harris' book may be taken to mark the formal development in England of entomology as a pastime. 'The Aurelian' gives a finely illustrated account of butterflies and moths and how to collect them. Originally published as a series of parts, each with a fine hand-coloured plate usually dedicated to a member of the nobility, its text was in English and French and it passed through several editions (Lisney 1960).

In the eighteenth century persons interested in entomology came together to form entomological societies, indeed perhaps the first in the World was the 'Aurelian Society' that existed in London in 1743, if not earlier: its books and collections, housed at the Swan Tavern, Exchange (now Change) Alley, perished in the great fire of Cornhill of 1748: the fire started in a nearby wigmaker's and the members narrowly escaped the same fate! The term 'Aurelia' had been used, since 1607, for the chrysalis of a butterfly. A succession of societies developed in Britain over the next hundred years, some were entitled 'Aurelian', others 'Entomological' (Neave 1933, Ford 1945). The Entomological Club, founded in 1826, still exists and is the oldest entomological organization in the World. Its membership has always been limited to 8 persons and its function is principally social. Its main impact nowadays is in the organization of the 'Verrall Supper' for entomologists held annually in London since 1912: it also 'spawned' the South London, now the British, Entomological and Natural History Society (James 1973).

On 31st January 1832 the Société Entomologique de France was founded and a year later, in March 1833, the (Royal) Entomological Society of London. These are now the oldest scientific societies and the great majority of the members of the latter are professional entomologists, but at the time of their foundation the professional entomologist hardly existed. It is interesting to examine the early membership of these Societies: of the 156 members in the first ten years of the Entomological Society of London, no less than eleven were noblemen, headed by a duke; there were only nine professionals – interpreting that concept widely enough to include Charles Darwin. A study of the membership list in *Bull.Soc.Ent.France* Vol. 1 shows a similar picture. Other national entomological societies were formed in Europe, towards the end of the nineteenth century. In 1906 national entomological societies were formed in Egypt and the USA; the former containing a majority of non-professionals, particularly lawyers. The Entomological Society of Ontario (= Entomological Society of Canada) started the publication of a national journal, the 'Canadian Entomologist' in 1868, five years after its foundation (Bethune 1868).

Very broadly the persons who established and joined these national societies had their primary concern in entomology in one of three main ways: as a pastime, as a branch of zoology or as the scientific basis for pest control. As I stressed before these are not mutually exclusive, but it is interesting to compare the strengths of the different components in various countries. A comparison

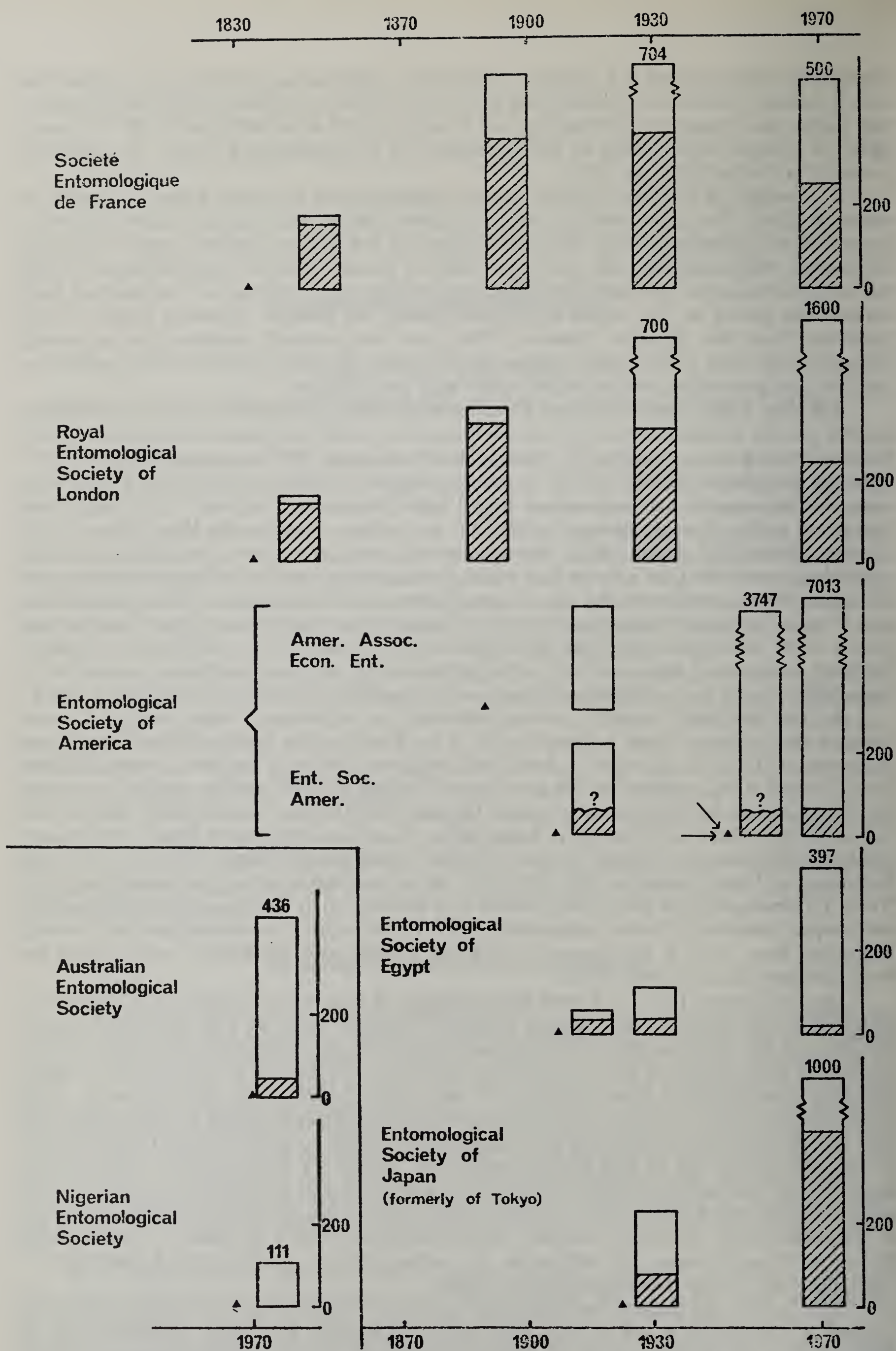


Fig. 1.—The growth and composition of the membership of various national entomological societies. (Shaded portion represent members for whom entomology is not their livelihood; triangles mark date of foundation).

of the amateur (= pastime) component in the membership of some national entomological societies is shown in Fig. 1. Three facts emerge:

- (i) Significant numbers of amateur entomologists are found in national societies only in Western Europe and Japan.
- (ii) Although the proportion of amateur entomologists in the European Societies may have fallen during this century, especially in the Royal Entomological Society of London, the actual numbers have not decreased significantly.
- (iii) In Japan both the proportion and actual numbers of amateurs seems to have increased.

I will speculate later on the causes of the early development of entomology as a pastime in Western and Central Europe and in Japan. In most parts of the industrial world many local entomological societies were founded in the middle part of the nineteenth century. In London for example there were several 'working mens' societies, often meeting in public houses.* In 1862 the "East London Entomological Society" met regularly at the "Bell & Mackerel." Of these only the "South London," now renamed the 'British Entomological and Natural History Society' still survives and a review at the time of its foundation remarked that it did not meet at a public house and "we believe the social position of the members is higher — but the working-man element is represented" (James 1975). During the Victorian era in Britain entomological exhibitions were regularly held, widely advertised and commented upon in the national press (Stanley-Smith 1953), whilst entomologists and insects often figured in cartoons.

In North America, likewise, some local societies were started (Sabrosky 1956, Gurney 1976) e.g., the Brooklyn in 1872 with 5 founders. The members of these societies, described as "wielders of the butterfly net or beetle bottle," were often clergy or teachers (Bethune 1868). Undoubtedly the collection of beautiful objects is a common practice in industrial countries becoming extended to all sections of society when their leisure time and housing conditions for storage, permitted this. However, as a writer in the (London) *Standard* newspaper of 19 October 1888 said "Entomology [is] of such scientific importance. In the days before Darwin a moth was simply a moth — one more addition to the corked drawers of the cabinet, another name added to the ever lengthening lists — But since the strange discoveries that led to Darwin's theory a Naturalist no longer values a 'specimen' simply as a 'specimen', but as a link between two others already known —. The important observations regarding mimicking among insects form an apt illustration of this." Thus the collectors pastime became transformed into the scientific study. Then, as now, the collection of insects frequently commenced in childhood, but once started the attractions of bionomic or physiological studies are realized (e.g., Wigglesworth 1965). The value of insects for science was comprehensively reviewed at the last Congress by E.H. Smith (1973).

Although, probably because of urbanization, entomology has not perhaps kept its comparative position amongst leisure activities in this century, it still flourishes. In Japan, as Dr. S. Iwao informs me, there are "many local entomological associations"; in North America there are specialized societies for Lepidoptera and Coleoptera and in Britain the predominantly non-professional British (formerly 'South London') Society has doubled its membership since the last War (James 1975). A measure of the general interest retained in, for example, butterflies in Western Europe may be gauged from the success of Higgins & Riley's 'A Field Guide to the Butterflies of Britain & Europe' (1970) which has appeared in eight languages and sold over 65,000 copies.

Economic entomology, the third component, first played a major role in one of the two parent bodies of our host society: the American Association of Economic Entomologists which was founded in 1889. For a long time this was the only entomological society whose founders and members were primarily concerned with the economic impact of insects on man. For the other nineteenth century societies this was a secondary interest, although as early as 1834 the (Royal) Entomological Society of London advised the sugar-cane growers of Grenada on the control of *Saccharosydne saccharivora* (Westwood). However, most societies founded in the last two decades, e.g., the Nigerian Entomological Society, have been more like the A.A.E.E. in approach: in the Proceedings of the first and second conferences of the Nigerian Society the emphasis is clearly placed on the applied aspects (*Proc. ent. Soc. Nigeria* vol. 1). The world-wide recognition of the value of entomologists to mankind has led to the growth of the entomological profession, the majority of whose members, I hope, enjoy

*'Public house' is a British term for houses that sell alcoholic drinks, i.e., taverns, beer cellars, bars.

their work and might in another century have been amateurs. The attendances at these International Congresses (Fig. 2) is some measure of the growth of our profession.

I would now like to consider briefly the early development of entomology as a pastime in Western and Central Europe and Japan, compared with the rest of the World. The principal factors involved seem to be:

- (1) The existence of an 'aristocracy' and a substantial professional middle class that had leisure and sought both to collect beautiful objects and to acquire knowledge.
- (2) Religious attitudes to nature and the taking life.
- (3) The ease of preserving collections.

The Société Entomologique de France was founded under the Presidency of M. Luczot, Chief Engineer for Bridges and Roads; Entomological Society of London under Mr. J.G. Children, the son of a banker, and the Librarian of Antiquities at the British Museum. These professional men, lawyers, doctors, engineers, bankers and, especially, clergymen, were soon joined by members of the nobility (as already mentioned these constituted nearly 10% of the membership). The importance of their role was not so much in their actual contribution to entomology, but in setting a general trend in collecting beautiful objects and accumulating knowledge. It is noteworthy that Moses Harris dedicated most of his plates to a member of the aristocracy. In the Netherlands in the same period, illustrations of European and South American Lepidoptera were being made and published by Maria Merian, Countess of Nuremburg. As we have seen other socio-economic groups would follow this lead, but although insects were (and are) auctioned, with skill, hard work and an element of luck, the poor clerk could obtain a better specimen than a duke. In Japan the same influences seem to have existed but for longer periods. From the 11th-12th centuries there is the story of Mushi Mezuru Himegimi (The Lady who Loved Insects), a princess who collected and reared insects (Konishi & Ito 1973), and today the Japanese Imperial family is active in zoological work.

Following St. Augustine, the western Christian could be further encouraged in his entomological work by regarding it as an act of piety. Both the title page and the frontispiece of the Aurelian have quotations from the Psalms (104 v. 24 & 111 v. 2). A different attitude prevailed in the Indian sub-continent: under the influence of the Buddhist and Hindu religions all life was revered. The cycle of reincarnation, as expounded in the Upanishads, includes insects. The Jain sect wore a cloth across the mouth so as to prevent their accidentally swallowing and killing a gnat. An offering of wheat may, even today, be placed for ants around their nests. The Muslim Mughal emperors adopted these attitudes and on the grave of the Empress Nur Jahan (who was a Persian noblewoman) is written, supposedly at her request, a verse that may be translated:

“Do not decorate my grave with flowers or candles
Because the flowers may deceive the song birds
And the candle may burn the moths”

In tropical and subtropical regions the actual maintenance of an insect collection is, as many here will know to their cost, a difficult operation and this must have been a powerful discouragement to amateur entomology in Africa, Malaysia and other areas.

Interest in Lepidoptera undoubtedly has an aesthetic element. In feudal Japan many fine Tyuhu (or Chu Fu) (Illustrations of Insects) were prepared (Konishi & Ito 1973). In 1785 Moses Harris, the author of “The Aurelian,” exhibited a “frame of insects” at the Royal Academy, presumably amongst the paintings of Reynolds, Gainsborough, and others. Parts of insects have been used as decoration and adornment in all parts of the world; Japanese and Korean shrines of the 6th century were decorated with buprestid elytra. Today they are used, especially in those sections of society for whom other cheap jewelry is unavailable. In India butterfly wings or beetle elytra may be utilized, sometimes as earrings or as an ornament (Tikli or Tella) on the centre of the forehead; in South and Central America they are commonly incorporated into jewelry and ornaments; whilst in parts of Mexico living specimens of large Cerambycids, painted and attached to a small chain and pin, are sold by street traders as a moving brooch.

The decorative value of insects was appreciated by the illustrators of illuminated manuscripts. There are quite remarkable representations of various insects (and other animals) in fourteenth and fifteenth century manuscripts. Among the more unusual species represented are the water boatman (*Notonecta*), the carpet beetle (*Attagenus pellio* L.) the firebug (*Pyrrhocoris apterus* L.) and a burnet moth (*Zygaena*) (Crombie 1952, Hutchinson 1974). Insects have figured in sculpture in many epochs

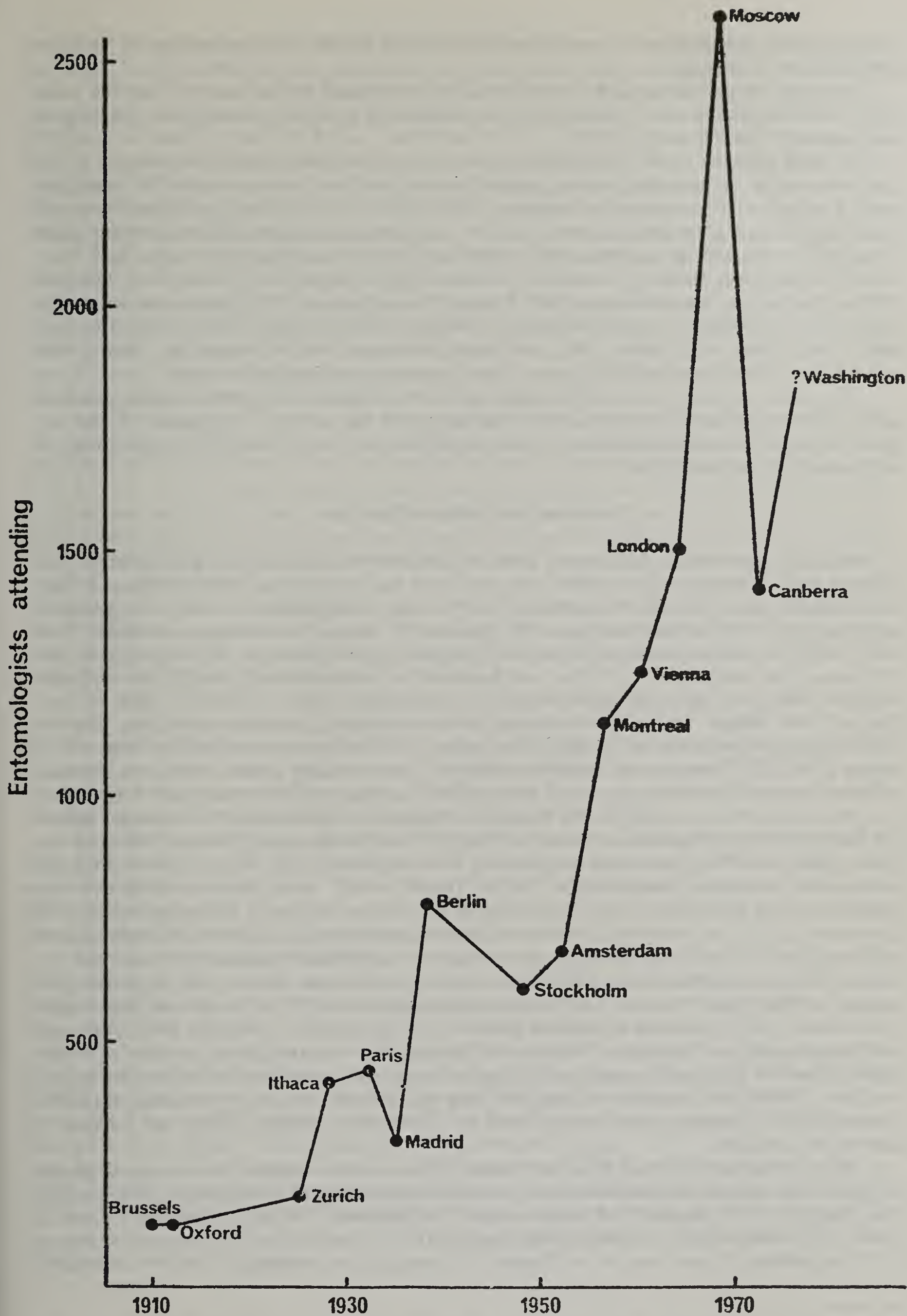


Fig. 2. —The number of entomologists attending International Congresses of Entomology.

and many areas: from Mexican terracotta fleas (200-800 AD) (Morge 1973) to the monarch butterfly at Pacific Grove, California!

Although various animals and plants have figured on postage stamps for more than 100 years (e.g., codfish and seal on the Newfoundland issue of 1866), it is only very recently that insects have been pictured* (Strom & Lewey 1968).

In 1930 Lebanon issued a series, figuring the stages of the silk moth (*Bombyx mori* L.) to commemorate the Sericultural Congress held in Beirut, after this it was not until 1948 that Chile issued a series (to commemorate the centenary, 1844-1944 of C. Gay's book on Chilean Flora and Fauna) that features *Chiasognathus granti* Stephens, a butterfly and a mantid. Since then many types of insects have figured on some hundreds of different stamps; sometimes whole series have been devoted to particular groups, for example, butterflies (e.g., Hungary 1959, Cuba 1965, Tanzania 1975) or beetles (e.g., Czechoslovakia 1962, Central African Republic 1962). Other issues emphasize applied aspects particularly malarial control (e.g., Dominica 1962, Ecuador 1963) or locust control (Mali 1964). Some (e.g., Japan 1966) are largely decorative, whilst France has featured the entomologist, J. Fabre and the USSR honored this Congress by a special issue in 1968.

One must conclude therefore that although the intellectual and artistic pleasure mankind derives from entomology is a comparatively small part of its role, it is very significant and with the spread of travel and the development of color photography and other relevant techniques, there is every reason why it should grow.

Insects and the Welfare of Mankind

Mankind undoubtedly first became aware of insects when they bit him! The genera of lice infecting man, *Pediculus* and *Phthirus* also occur on the apes (Buxton 1939) and so at that undeterminable time when *Homo sapiens* L. first became distinguishable his lice were probably making him itch! The medieval method a wife should use to de-louse her husband, described by Von Caub (1480), in Hortus Sanitatus, shows only marginal improvements on the technique of the chimpanzee (*Pan troglodytes* L.)! Fleas and bugs are less intimately and possibly less anciently associated with man; the more primitive forms of both groups seem to be ectoparasites on bats (Holland 1964, Usinger 1966). With bed bug (*Cimex lectularius* L.) it seems most likely that the transfer occurred somewhere in the Middle East region, when man was a cave-dweller (Sailer 1952, Usinger 1966): the Cimicinae are virtually restricted to cave dwelling animals: man, bats, pigeons, swifts and martins. There is no conclusive evidence that bed bugs transmit a disease and it seems that it is only comparatively recently, in the fifteenth and sixteenth centuries, that *C. lectularius* spread into Western Europe. [A pronotum found in a Roman site in Britain could, however, belong to this species (Osborne 1971)]. All these ectoparasites were widespread and often abundant until the development of modern insecticides in 1940-6. Tribute to the Aztec emperors of Mexico was sometimes paid in lice (Morge 1973). When Thomas Beckett was undressed, following his murder at Canterbury in 1170, his innermost garments of haircloth seethed with lice 'like water simmering in a cauldron' (Stanley 1906). Contemporary chroniclers, such as William Fitzstephen, who reported this regarded it as an additional sign of saintliness, so we may surmise that the size of the population was unusual for those times. However, even less than 40 years ago nearly 50% of the female children aged 2-13 and even 5% of the adults in a British industrial city had head lice (Mellanby 1941). Although these ectoparasites were ubiquitous mankind was clearly by no means indifferent to them: a Chinese pharmacopoeia of the second century recommends mercury and arsenic for the control of body lice, von Caub (1480) gives remedies for lice and fleas and perhaps the first professional economic entomologist was Londoner, John Southall, who ran a business controlling bed bugs and published a book on them in 1730.

Many insects are vectors of important diseases. The tremendous impact of epidemics of plague and typhus and endemic malaria on mankind are well documented (Bell 1924, Zinsser 1935, Barraud 1956, Brighetti 1968, Ziegler 1969, Scarborough 1970, Shrewsbury 1970, Garnham 1971, Glass & Reville 1972, Cipolia 1973, de Zulueta 1973, Harrison 1977). The magnitude of the impact of plague on the population of man must be emphasized: for example the pandemic of 542-594 AD killed

*A butterfly adorns the hair of Queen Liliuokalani on the Hawaiian 2c. of 1862 and a termite mound illustrates the 35c. Somalia of 1932.

about half the population of the Roman Empire, and a similar proportion were killed in England in the 'Black Death' (1348-9); these proportions compare with a death rate of under 6% in the most heavily affected areas in the First World War (Serbia and Montenegro) (Kosinski 1968). Typhus was the great killer when men were herded together and so armies were especially affected. The prevalence of malaria in ancient Rome, transmitted by the mosquitoes breeding in the surrounding marshes, is sometimes considered to have contributed to the fall of the Roman Empire (Celli 1933). Insect-borne diseases have also had their impact on history through the deaths of men of great influence: Alexander the Great seems to have died of malignant malaria and Oliver Cromwell died with quartan malaria (Garnham, pers. comm.).

Today insect-transmitted diseases are still widespread. It is estimated that at present 300 million persons in the World are suffering from filariasis, 200 million from malaria and 10 million from trypanosomiasis: thus about one in seven of mankind has one or the other of these particular diseases.* The magnitude of the importance of these insect disease vectors to mankind need not be elaborated and many papers at this Congress will be devoted to them. One should note, however, that recently some influential bodies are advocating a policy that emphasizes a biochemical attack on the pathogen itself rather than work with the vector (Dorozynski 1976).

An examination of the range of insects described by Aristotle (Peck 1965), by Pliny the Younger (Holland 1635) and by von Caub (1480) gives a clear picture of those noted by men in their everyday lives. The first group of the ectoparasites described above have literally been with man since prehistory. The second group, headed by the honey bee, concerned those insects that provided food, medicine wax and silk for man and the third group those that we would regard as pests: locusts, cankerworms and gnats, as well as woodworms and moths from 'wool and cloth when they be dusty' (Pliny, after Holland 1635). It is of considerable interest that at this time the number of insects regarded as useful seems to have been not much less than those noted as harmful: Pliny devotes nearly as much space in the Eleventh Book to the Honey bee (*Apis mellifera* L.), as to all other insects together. In contrast in 'Applied Entomology' (Fernald & Shepard 1921) over 80% of the pages that give specific accounts, refer to harmful species, although the authors note that "the benefits to man (of insects) are frequently overlooked."

The role of insects as sources of medicine, clothing and food has been diminished by new knowledge and new techniques. The Stag Beetle (*Lucanus cervus* L.) was unlikely to prove an effective remedy "against many maladies" as suggested by Pliny, but *Lytta (Cantharis) vesicatoria* (L.) is still recognized as producing a venom "howbeit medicinable in some sort" (Pliny). The major entomological work in ancient China was Li's (1596) Great Pharmacopoeia which gives a remarkable classification, as well as hundreds of medicinal uses (Konishi & Ito 1973).

The silkworms (*Antheraea*, *Bombyx*, *Philosamia*) have had an important role in the history of mankind from at least 4700 BC (Konishi & Ito 1973): silk was a major factor in encouraging trade and travel between East and West: Marco Polo (1294-1324) refers to it in the same way as silver and gold. The importance of silk is now much reduced, but in some areas, like Assam, every home will have a loom and it is part of a girl's upbringing to be able to weave silk.

The honey bee (*Apis mellifera* L.) is another insect whose importance to man has been recognized from the earliest times. Honey was a relatively more important food prior to the availability of sugar from cane (500 BC in India taking about 2000 years to spread to S.W. Europe) or from beet (1800 AD). Bee combs and honey gathering are figured in cave paintings from Spain, Australia, India and Southern Africa (Hernandez-Pacheco 1921, Pager 1973, 1976). Scutiforms, representing combs and ladders are common themes and those from Altamira, Spain are probably 20,000 years old. A rock painting from the Matopo Hills in Southern Africa clearly shows 'smoking a bee's nest' (Pager 1976). The importance of the bee was such that it became part of religion and lore (Edwardes 1911, Wheeler 1923, Ransome 1937, Townsend & Crane 1973). Reference has already been made to its representation in Ancient Egypt, but the hymenopteran depicted on the Minoan golden pendant is considered by entomologists to be a *Polistes* (Richards 1974). In medieval Europe the honey bee was still important; it is considered that the common heraldic symbol, the 'fleur-de-lis,' may represent a bee, head downwards: it is now used as the colophon on the Annual Review of Entomology (see Vol. 19, p. 5).

*At least one in six are suffering from some insect-borne disease.

Insects themselves were, judging from the ancient literature, more significant for food in the past than today. Aristotle (Peck 1965) advises that the male Cicadas are tastier when young, but the females are preferable later when they are full of eggs. American Indians and Australian aborigines also consumed cicadas. The latter often relied heavily on insect food including the honeypot ant (*Melophorus*) and the 'witchetty grub' (Hepialid and other large larvae) (Campbell 1926, Bodenheimer 1951). Even insect eggs may be eaten: in the lakes near Mexico City the eggs of various water bugs (Notonectidae and Corixidae) are collected on special rush traps and sold as 'ahualte,' whilst the adults are collected in nets, dried and sold as 'moschitos.' For a period John the Baptist probably depended entirely on insects for his food: 'he did eat locusts and wild honey' (St. Mark 1 v. 6). Large orthopterans are still an important item of diet, especially for children, in certain parts of Africa: locust control programmes need to take cognizance of this (Richards 1975) and various recipes for locust dishes are given by Abdullah (1973). The above are just a few diverse examples; entomophagy is advocated by Holt (1885) and the whole subject is well reviewed by Bodenheimer (1951) (see also Brues 1946 and Abdullah 1973).

Today our predominant concern in relation to insects and food is usually the food that they consume, although the role of pollinators, parasites and predators is not overlooked. Locusts are particularly spectacular defoliators and it is not surprising that their plagues have wrought wonder and anguish in the hearts of men from early times. They are shown eating cereals on a Mastaba erected towards the end of the Old Kingdom in Ancient Egypt (c. 2300 BC). Many of the ancient writers refer to locusts; often to various caterpillars and Pliny even mentions 'flies from radish roots and other little grubs likewise in lettuce and beet leaves' (Holland 1635, Meyer 1959, Harpaz 1973). Stored products pests, although not widely commented upon in contemporary writings, seem to have been widespread in ancient times (Solomon 1965, Osborne 1971, Burleigh & Southgate 1975).

Today the range and magnitude of pest damage to our crops is well recognized. The value of insecticides applied in a single year probably approaches \$2,000 million (Lewis 1977). Cramer (1967) estimated world crop losses at 10-15%. As about 20% of the ever-growing population of mankind is without an adequate food intake (Ehrlich & Ehrlich 1970) and insect losses tend to be heaviest in just the areas afflicted by malnutrition, we can claim that the proper practice of applied entomology has a vital role in the future of mankind (Pimentel 1975) (Fig. 3).

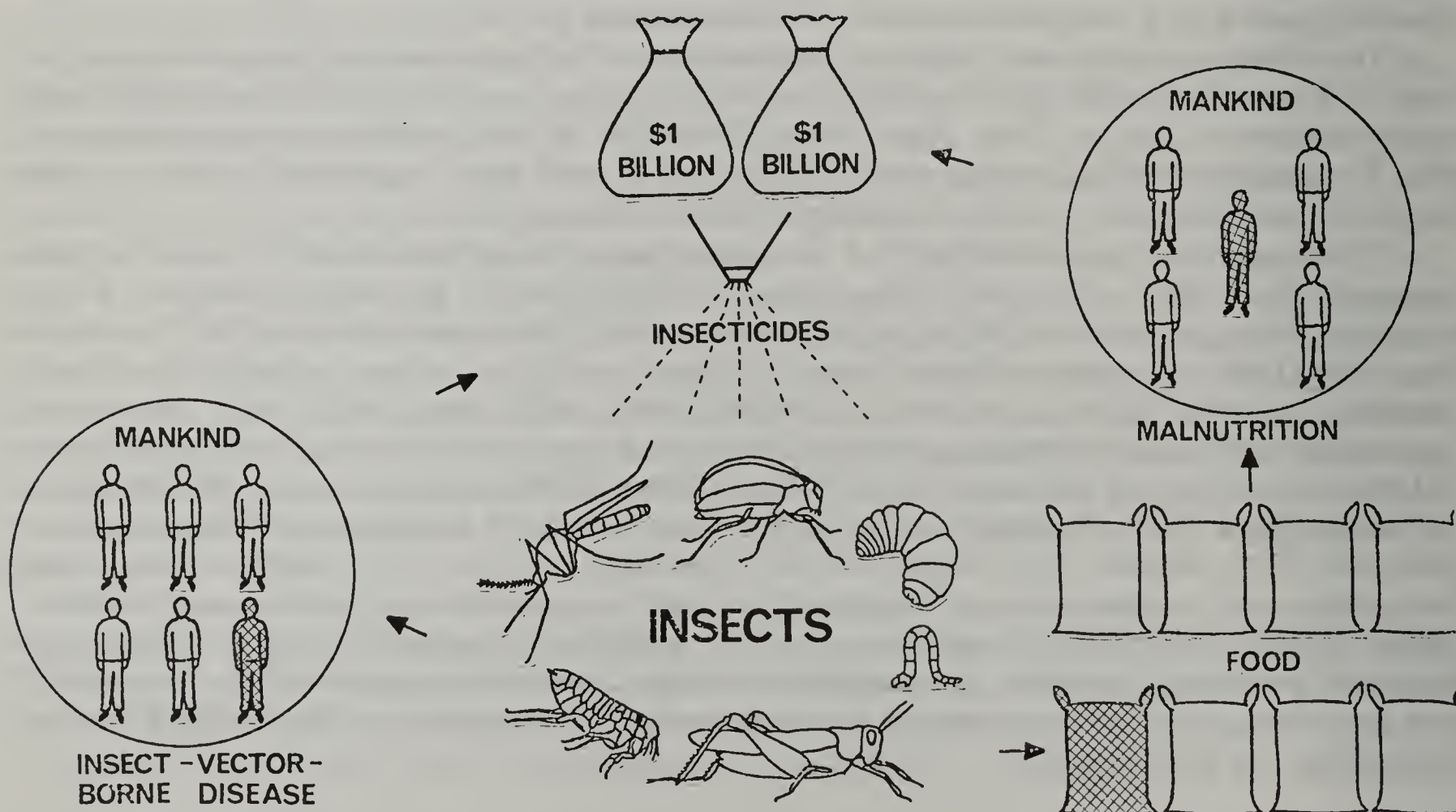


Fig. 3. --The impact of insects on the welfare of man.

The Co-existence of Mankind and Insects

After pointing out that about one in six of mankind is suffering from insect-borne diseases and that one in five is malnourished, whilst insects consume enough food to satisfy these needs, co-existence may seem an odd choice of words. You may feel McKelvey's (1975) concept of our task "to banish those insects which, as pests, are doing us more harm than good" is more appropriate. However, banishment or eradication must, I think, remain the exception rather than the rule: this is because the costs are too high. In this final section I wish to explore the strategy of this co-existence and from this explanation I believe the justification for my view will emerge.

Whether a particular species of insect has pest status in an area will depend on (a) its numbers and (b) the sensitivity or tolerance of the victim (crop, animal, person). From this it follows that an understanding of the principles that underlie the population dynamics of pests is an important component in a pest management scheme.

During the last few years progress has been made in understanding the essential dynamical features of insect populations (May 1976). Both single and multiple species systems may show a range of dynamic behavior depending on the magnitude and relationships of certain parameters in the relevant population equations (Hassell & May 1973, May, Conway, Hassell & Southwood 1974, May 1975, Hassell, Lawton & May 1976). The magnitude of certain of these parameters, intrinsic to the insects, are clearly the result of evolutionary selection; the templet for these, on theoretical grounds supported by the analysis of the life tables of 32 different insects, appears to be the durational stability of their habitat (Southwood, May, Hassell & Conway 1974, Southwood 1975, 1976). Durational stability is defined as H/τ , where τ = generation time and H is the length of time that the habitat location remains suitable for breeding. The H/τ spectrum relates to the r-K continuum (MacArthur & Wilson 1967, Pianka 1970). Basically those species with habitats of low durational stability are r-strategists: they tend to be small, mobile and with a short generation time. Species with

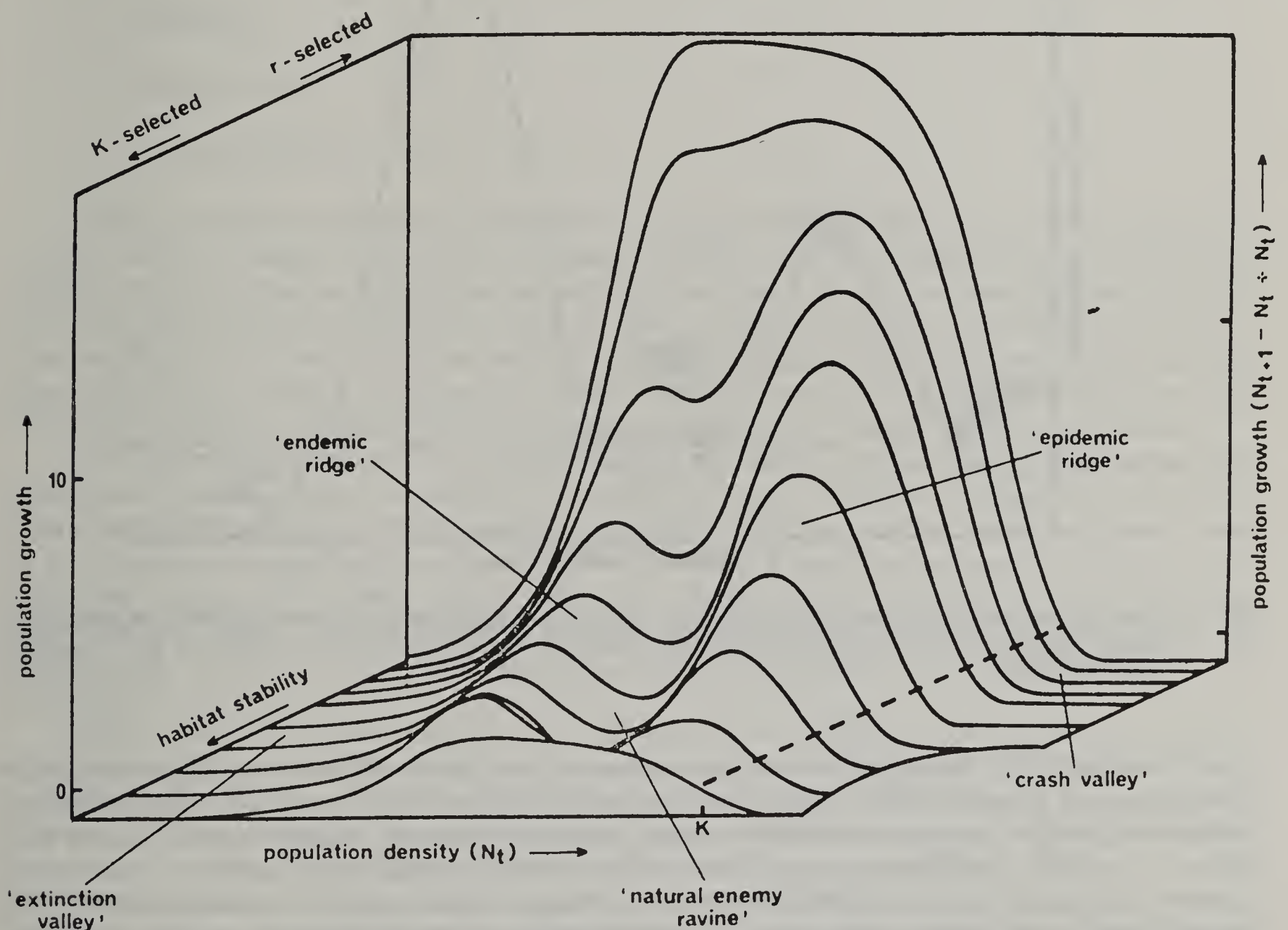


Fig. 4. —The synoptic model of population growth with axes for population growth, population density and durational stability of the habitat (after Southwood 1977).

stable habitats (high values of H/τ) are towards the K-end of the continuum, they are larger, more likely to be territorial than migratory and have a long generation time.

It is therefore possible to construct a three-dimensional synoptic model, that illustrates the basic features of population growth in relation to population density for species at different points in the r-K continuum (Fig. 4) (Southwood 1975, 1976, Southwood & Comins 1976). The precise position of a species on the r-K continuum is flexible and responsive to evolutionary pressures. The adjustments and readjustments depend on the processes of genetic feed-back clearly propounded by Pimentel (1961, 1968 and Pimentel & Soans 1971). An important feature of this model is the 'natural enemy ravine' that is deepest at the intermediate position in the r-K continuum and dips below the zero growth contour. This is because there are two stability points for the populations of these species: an upper one determined by competition and a lower one determined by natural enemies (Fig. 5) (Southwood 1975, Hassell 1976, Southwood & Comins 1976). Populations of, for example, forest insects often remain at comparatively low levels for much of the time: that is they are held in the domain of stability (Holling 1973) of the natural enemy stability point (S). However, from time to time an environmental disturbance allows the populations to escape from this equilibrium level, past the release point (R) and rise to a much higher density (U): an outbreak occurs. This is exactly the situation described by Clark (1964) for the eucalyptus psyllid, *Cardiaspina albitextura* Taylor, and its dynamics can be described in terms of this model (Southwood & Comins 1976). When the European spruce sawfly [*Diprion hercyniae* (Hartig)] was first introduced into Canada, its population, free of all natural enemy control, rose until limited by competition; but the combination of parasites and a virus disease reduced the population level (Balch 1939, Bird & Elgee 1957) and the lower equilibrium level was established (Southwood 1977).

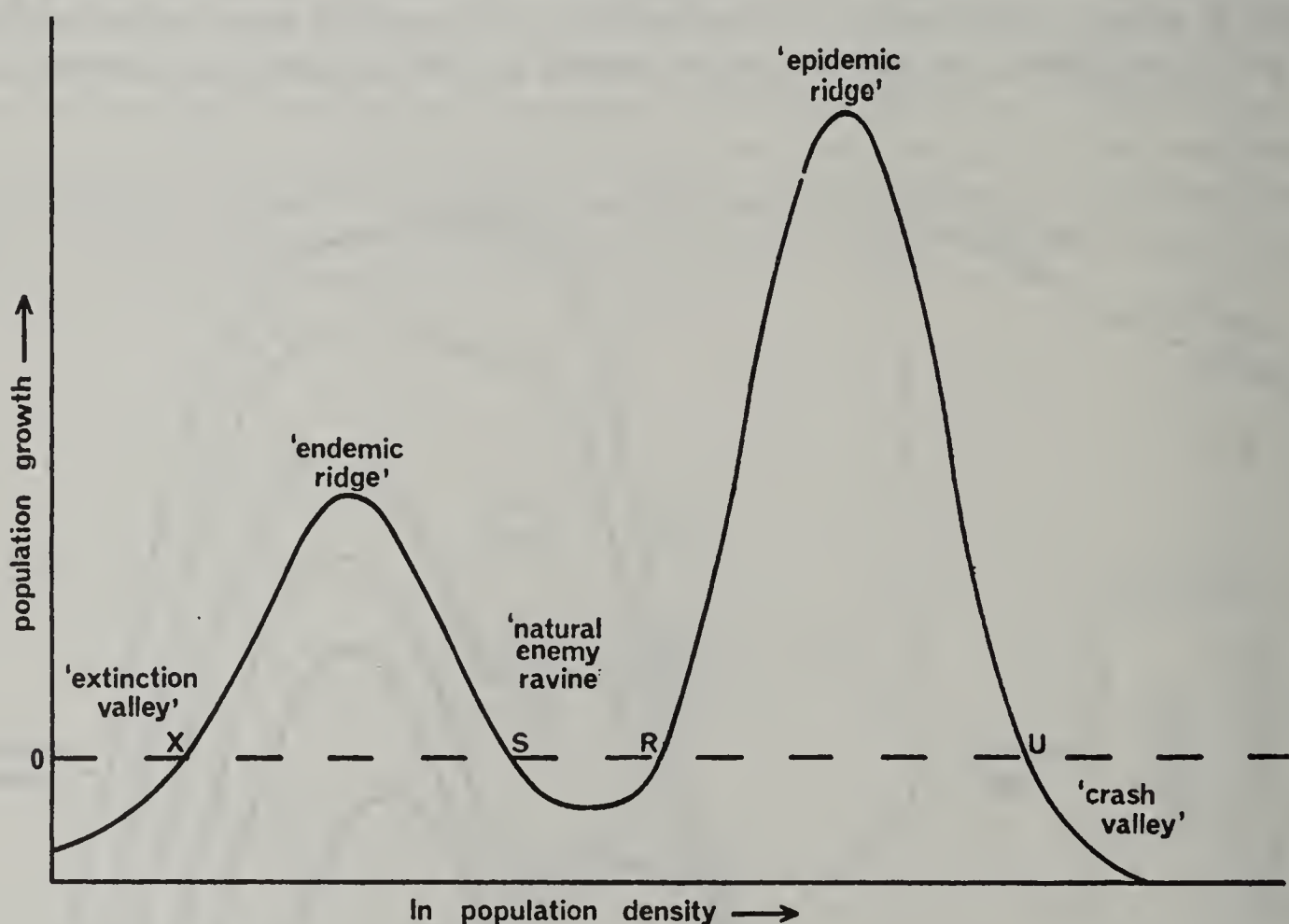


Fig. 5. —A section through the 'natural enemy ravine' of the synoptic model with two stable equilibrium points (S — natural enemies; U — intraspecific competition) and two unstable points (X — extinction; R — release to epidemic levels).

Conway (1976) has suggested that the concepts from this model may usefully be applied to pest species and I have been able to elaborate the idea (Southwood 1977). *r*-pests are characteristic of habitats with high durational instability — desert locust, *Schistocerca gregaria* (Forskl.), house flies (*Musca domestica* L.). Their strategy is one of boom and bust; the 'bust' holds no evolutionary penalty because that particular habitat location is no longer tenable, members of the species will have migrated and some will have found new sites (Southwood 1962). Natural enemies are of little significance, *r*-pests will virtually always achieve pest level if enough of them invade the crops and there is adequate time before harvest.

K-pests in contrast will occur in more stable habitats: their reproductive rates will be low and their population fluctuations will be small compared with *r*-pests. The codling moth [*Cydia pomonella* (L.)], the tsetse flies (*Glossina* spp.) and various large Bryocorine mirids that attack cocoa in West Africa and the Far East are typical examples. A *K*-pest's normal harvesting has no significant deleterious impact on the supply of its natural food, [n.b. cocoa is not the original host of the mirids (Leston 1970, Conway 1971)]. However, if this level of harvesting is intolerable to man, as codling infestation of apples is, then such species are virtually always pests.

In between these extremes are the majority of deciduous forest insects, fruit insects and some vegetable pests. These are for much of the time held at a lower equilibrium point by natural enemies, but when they escape from this 'natural enemy ravine' they reach outbreak level and become pests. Those near the *r*-end, like aphids, escape most frequently.

This knowledge we have of the basic underlying population dynamics of different pests gives useful indications of the appropriate pest control methods (Conway 1976, Southwood 1977) (Table 1): control being used in the sense of reducing the impact of pests so that the marginal cost of further measures will be more than the marginal revenue gained from the further increment in yield (Southwood & Norton 1973, Conway & Norton 1977).

Table 1.—Indications for control methods in relation to ecological strategies of pests.

<u>Control Method</u>	<u><i>r</i>-pests</u>	<u>Intermediate pests</u>	<u><i>K</i>-pests</u>
Insecticides	+++		++
Natural enemies.		+++	++
Cultural	++	+	+++
Reproductive		+	+++
Host resistance	++	++	++

r-pests are always fluctuating and therefore any appeal to the stability of natural ecosystems is spurious and foredoomed to failure (van Emden & Williams 1974, Southwood 1977, Way 1977). Cultural control techniques will depend on reducing the chances of pest invasion (Southwood & Way 1970) by, for example, increasing the scale of the monoculture and so heightening the degree of isolation (Way 1974). But in these inherently 'booming' populations insecticides will remain the most powerful technique: their rational use will demand the development of better methods of forecasting (Way & Cammell 1973, Benedek 1975) and assessing (Matthews & Tunstall 1968) pest outbreaks.

The appropriate strategy for intermediate pests will depend on maintaining them below their release point, in the domain of stability of the natural enemy equilibrium point (S). These are the pests where biological control or integrated control with a significant natural enemy component must be the dominant strategy (e.g., van den Bosch et al. 1971). The regular prophylactic application of insecticides to such pest systems will eliminate the natural enemy ravine: hence the outbreaks of 'secondary' or 'upset' pests (Entwistle, Johnson & Dunn 1959, Conway & Wood 1964) are consequences of such an ill-advised approach, called by Newsom (1975) a "womb to tomb" programme.

The *K*-pest will be most sensitive to the disturbance of its habitat; it will often have complex reproductive tactics and these with the low recruitment rate of the adult stage lead to a broad extinction valley in the synoptic model (Fig. 4). The majority of *K*-strategists fail to adapt to man-made environments, but those that have may be controlled by a variety of methods, particularly reproductive techniques involving sterile males or the use of pheromones (Roelofs 1975).

Host resistance is valuable for all pests; it may be thought of as decreasing the rate of population advance across the synoptic landscape. More precisely it reduces the finite natural rate of increase, the effect of which is shown in Southwood & Comins' (1976) simulations.

From this survey you will see that I consider insecticides are a vital tool in our co-existence with insects: we cannot do without them, but they do not provide the whole answer. When the

tactics of any particular pest control operation are being considered the cost of control is a major factor. The costs of an insecticide are:

- (i) the cost of the material.
- (ii) the cost of application.
- (iii) 'external costs' — their influence on non-target organisms, etc. (Langham & Edwards 1969).

Fortunately increasing attention is being paid to external costs; here in the USA, a legislative framework is developing (Deck 1975). The cost of insecticides themselves, in spite of recent increases, remains modest. However, the costs of developing new pesticides are fearsome, probably in the region of \$15-20 million at current prices, and there is clear evidence that the number of new products being introduced has fallen markedly (Lewis 1977). It is therefore in the interests of all concerned that the 'life' of the available insecticides should be as long as possible.

The useful life of an insecticide may be terminated by the widespread development of resistance in target organisms or by the saturation of the ecosystem so that non-target organisms are affected and the product becomes banned, as has happened in many countries with DDT and several other compounds. Many factors influence the development of resistance and the attainment of significant damage to the ecosystem, but in general terms they are both proportional to the quantity and the rate of usage of the particular insecticide (Smith 1970, Way 1971, Adkisson 1973, Comins 1976). Forecasting and the assessment of pest level, referred to above as well as new techniques (ULV, granules, etc.) that greatly reduce the quantity of insecticide applied per unit area (Kiritani 1974, Jepson 1976, Matthews 1976) are important in our attempts to prolong the life of an insecticide. Routine use and overkill must be avoided: the health dangers and the agricultural risks of a breakdown in the availability of insecticides are very great. This has been emphasized by Drs. Pal and Brown (1974) of WHO and by the recent National Academy of Sciences Committee under Professor Donald Kennedy (Carter 1976).

Against this background we can return to the question of banishment or eradication as it is commonly called. The basic characters of the population dynamics show that *K*-pests, with their wide extinction valley, are indeed vulnerable to eradication: especially by habitat modification. Unfortunately most *K*-organisms are just those we wish to conserve: many tropical rain forest butterflies and, extending beyond insects, birds such as condors and albatrosses. Other species will 'bounce back' from very low population levels and even if locally exterminated the remarkable dispersive powers of most insects, that are not at the *K*-end of the continuum, will ensure recolonization. Eradication programmes based on insecticides inevitably involve their heavy, widespread and prolonged use (Loftgren, Banks & Glancy 1975): experience has shown that because of this these programmes tend to squander a valuable resource — the life of the insecticide.

In conclusion as we look to the future one can see new vistas and an ever widening role for entomology in the service of mankind. We will continue to co-exist with insects using an increasingly sophisticated range of techniques. Pest management will develop a theoretical as well as an empirical basis. We will learn the lesson that pesticides are precious; their benefits may be so easily curtailed by wanton application. We must be precise not profligate in their use.

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Entomology and the Problems of the Tropical World

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ABSTRACT

In the address to the Closing Plenary Session of the Fifteenth International Congress of Entomology, the author re-examines the traditional view of entomology and rejects it as a restrictive one. He advocates a more concentrated attack on a deep understanding of insects in their ecology, physiology, genetics, relations and interactions with other living organisms, and other specialized facets of insect life, leading to a recognized "insect science and technology." In this respect, he believes that insect scientists and technologists should be concerned with "insect livestock" — just as they are presently concerned (and over concentrating) on insect pest management. Finally, he pleads for a recognition that the tropics is the original and preponderant home of insects, and that a study of insects must naturally mean a major study of tropical insects in situ.

As one reflects on the advances of the study of insects over the last thirty years or so, one becomes uneasily aware of the tremendous reputation the insects and their close relatives, the mites and ticks, have acquired as pests of man, his crops, and his livestock. The discovery of DDT, with its spectacular killing powers, its persistence, and its wide spectrum of insect targets, tended to put in the hand of man a new weapon of a bully — for clubbing to death all insects and sundry, friend and foe alike. It has become all too easy to regard any insect one meets with as a pest. Indeed, we have become brutalized in the course of our indiscriminate killing of our insect co-inhabitants of the Planet Earth.

"Entomology" is supposed to mean the study of insects in all the facets of their lives in relation to the environment, just as "ecology" signifies the study of living things in relation to their environment. Yet, there is hardly any professional entomologist who does not derive his primary livelihood through the killing of insects, or the study of how to kill insects, or the training of younger colleagues who will do the job for him in later years. We, the latter-day entomologists, are living a kind of apologia, in which we (or at least a majority of us) attempt to tell the world (and to deceive ourselves in doing so) that the principal reason why we devote so much intellectual capital in the study of insects is really in order to know how best to kill them. Perhaps we do.

But perhaps we do not really mean what we tell the world. We are like Pain (1953) who found the world of beetles much more engaging than there being regarded merely as pests. In his little book, *Lesser Worlds*, he describes beetles in almost poetic terms:

"There are, in fact, all kinds of beetles, pleasant and unpleasant. The varieties are endless and it is impossible to come to any general conclusions about insects differing as widely in their habits and their way of life. And yet, when all is said, one is left with a feeling of affection for beetles.

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One remembers the common black beetle of the garden, plodding laboriously through the soil, the shining beauty of the sweet-smelling musk beetle, the unassuming lady-bird destroyer of garden pests. One remembers the curious glow-worm switching on her light to draw her love to her side and discreetly extinguishing it again when he reaches her — although none knows how she does it; and the alarming Bombardier Beetle, defying his enemies with volleys of artillery accompanied by audible pops and puffs of smoke. Above all, in this remorseless savage world of the insects, one salutes the domestic virtues of that humble Dung Beetle, the *Sisyphus*, so attentive to his mate, so hard-working for his children.”

It would seem that the honest thing to do is to admit to the world (and to ourselves) that we do love to study insects for the sheer joy of trying to understand this fascinating world; and that, as a dividend arising from this knowledge, we are prepared to assist in the killing of or controlling that very small proportion of the total insect fauna that is directly harmful to us.

Estimates of the number of insect species known vary considerably. But in tropical Africa, which is one of the principal homes of insects in the world, it has been thought that there might be well over 3,000,000 species. Of that number, only about 0.3% are major pests of man, his crops and his livestock.

“Yet, this small number commands the most concentrated attention of mankind. To be a ‘dudu’ is almost synonymous with being a nasty, wicked, pestiferous being; it seems that to be a ‘duduman’ is almost as noxious. Yet, many of these dudus are not only beneficial to man (e.g. bees, insect pollinators of horticultural crops, insect predators of other dudus), most of them could not care less about our existence one way or the other” (Odhiambo, 1975).

A way out of this dilemma is for us to systematically compile a balance sheet for the insect species that we do know well:

- Are they harmful to us (or our crops and our other products)?
- Do they help us in any other way — like being eaten, like producing products that we like to use, and like protecting us from our enemies?
- Do they completely ignore us?
- Are they worth knowing? Does knowing them add to our total sum of knowledge of the world?
- What is the secret of the success of insects in the present tropical world?
- How much concern do we cause insects, and how much do we benefit them?

If we ask ourselves these sorts of questions, and set about getting solutions to the latter for entry into our balance sheet, then we will truly be transforming entomology into a mature science and its application — INSECT SCIENCE AND TECHNOLOGY.

This notion of entomology is not a common one. Indeed, our present preoccupations with the problems of food production and the major tropical diseases (such as malaria, trypanosomiasis, and filariasis), where insects play a major and often a crucial pestiferous role, bludgeons all our finer judgements into accepting only the debit side of the insect/man equation. Yet, we must endeavour to reject this traditional insect world-view; we must remove the blinkers from our eyes so that we can look at the whole landscape and the horizon yonder of the insect world. It was Fabre who first expressed in 1918 this naturalist’s truth in his inimitable manner in his book, *The Sacred Beetle and Others*:

“It is a good thing from time to time to wield the hatchet in the overgrown thicket of tradition; it is well to shake off the yoke of accepted ideas. It is possible that, cleansed of its obscuring dross, truth may at last shine forth resplendent, far greater and more wonderful than the things which we were taught. I have sometimes harboured these rash doubts; and I have no reason to regret it, notably in the case of the Scarabad. Today I know the sacred pill-roller’s story thoroughly; and the reader shall see how much more marvellous it is than the tales handed down to us by the old Egyptians.”

The drama of tropical human life in the tropics is the drama of co-habitation, the drama of “insect bite man,” and the drama of “man eat insect.”

The Insect/Man Interphase

One of the closest non-human associates of man is the louse. The latter has co-habited with or actually parasitized our ancestors since pre-human times. The various species of louse have become closely dependent on man; they have become restricted to human blood for their sustenance, and die

within a few hours of the death of the human host because they cannot live on the cold body nor can they fend for themselves in the open environment. There are also another 250 species or so of sucking lice, which are likewise found living exclusively on the blood of other terrestrial mammals (with the exception of the carnivores, the dog family, and the marsupials). Just as with the human louse, they spend all their time on the skin of their hosts. It is of great biological and sociological interest that each louse species is restricted to a single host species, or a few very closely related host species. Indeed, one can identify the species of a host by the kind of louse species it harbours.

One of the great attractions of the study of human lice is to obtain an understanding of the intimate relationship that has developed between man and his lice fauna in the course of the long parallel evolution of the two groups of living animals. The living human species, *Homo sapiens*, carries two species of lice – crab louse (*Phthirus pubis*) which inhabits the human body hairs, especially in the pubic region), and two closely related subspecies of body louse (*Pediculus humanus humanus*) and the head louse (*Pediculus humanus capitis*). The two latter forms are almost identical in morphological terms, but are easily differentiated according to their habits. While the body louse lives mainly on clothing, especially near to the skin, the head louse lives in the hair of the head. Under experimental conditions, the two forms can be successfully interbred; but under normal circumstances in its natural habitat the two forms have little opportunity for cross-breeding and the incidence of this must be regarded as very rare.

An intriguing fact is that, for practical ecological purposes, the human louse fauna regards the human body as a complete ecosystem. Firstly, as we have seen, the three forms have circumscribed for themselves three distinct micro-habitats (and the attendant ecological niches) within which they live, feed, and reproduce during their entire life-cycle. The crab louse is largely confined to the pubic region, a universally available micro-habitat; and it is therefore not surprising that the crab louse is nearly world-wide in distribution, as it becomes transmitted to others through pubic contact. It is, in fact, rather uncommon throughout its range, although it has become much more common since the beginning of the 1960's – which may well provide a running commentary on the changing social behavior patterns of mankind. While the other two human louse forms are transmitters of louse-borne typhus and relapsing fever, crab lice causes no other unpleasant surprises to its host other than the need for scratching produced by irritation through lousy bites. It is within the realm of speculative louse biology that the crab louse has co-evolved with man for so long, and from such early times, that it can safely be regarded as having attained a symbiotic or mutualistic relationship. In contrast, the body louse seems to be a comparatively recent insect associate: it is carried from an infested person to another through clothing (especially that worn next to the skin). Clothing is a relatively new invention of man, who, in any case, possesses a naked body that is only covered by hair in a few strategic areas. It is possible therefore that the body louse is a recent migrant from the closely related head louse, from which it has genetically drifted as a result of behavioural and other isolation mechanisms. An observation that may well support this hypothesis is that the body louse can act as a carrier of typhus (and also of relapsing fever) – although in the course of doing so the infected lice, which carry the causative agent of typhus, *Rickettsia prowazeki*, die of the consequences of harbouring the rickettsiae. The latter multiply in the louse's gut, invade the stomach epithelium, burst through it into the body cavity, which leads to a quick death to the infected lice. The head louse, on the other hand, is not a natural carrier of typhus or relapsing fever, although it can be experimentally induced to transmit these diseases.

The second line of evidence that the human louse fauna regards the human body as a complete ecosystem is to be found in surveys of lice resistance to DDT and other de-lousing pesticides. For instance, in surveys carried in 1951 among a large group of Korean military personnel, it was a routine procedure to dust each military clothing-ware with DDT before it was worn. A long series of tests showed that body lice developed high resistance to DDT, whereas head lice retained their normal susceptibility (Brown and Pal, 1971).

Just as human evolution over the last 2.0 million years or so has been distinguished more by changes in behaviour than in anatomy – the making of tools, the habit of eating the meat of vertebrates, food sharing, domiciliary design and construction, the habit of living in group settlements, and many other traits that became distinctly “human” in the course of time – so the evolution of human lice has taken a parallel orientation, being more in the nature of specialization to exploit the peculiar advantages of available micro-habitats (pubic region and the head), and the harnessing of new opportunities thrown up by the evolving man (for example, clothing).

Is it possible that one way of tracing the origin and evolution of man may well be to look at the

Slides for cytological examination were prepared according to the technique of Rai, McDonald and Asman (1970). Rings or chains of four chromosomes indicated a single translocation heterozygote. Heteromorphism of chromosome arms in the translocation heterozygotes indicated an exchange of unequal segments.

Pre-adult mortality figures were obtained from the ratio of the number of adults produced to number of eggs hatched. In determining hatchability for each cross, all eggs on an egg paper were counted. For numbering the translocations, a system was adopted similar to that used by the Committee on Standardized Genetic Nomenclature for Mice (1963), and it is suggested that this nomenclature should continue to be utilized for *A. aegypti* in the future. The chromosomes which are translocated are given first, then a number indicating the order in which the translocation was identified, followed by the initial of the investigator responsible for its isolation.

Two sets of control crosses were also established. The first set involved non-irradiated males and females of the DELHI strain crossed to JY testers. The second set involved males and females, irradiated at 2000 r but not translocated, crossed to JY testers. Both sets of controls were evaluated for fertility, pre-adult mortality, wild-type marker transmission and crossover rates.

Results

Backcross Data

Data from 852 backcrosses to the JY stock of F₁ progeny of irradiated males are given in Table 1. The data are subdivided according to the sex of the F₁ test individual and the radiation dose used. A radiation dose effect on F₁ fertility was indicated. As the dose increased the overall average hatch of the backcrosses significantly decreased from 68% at 2000 r to 52% at 3000 r and 44% at 3500 r (p<.001). Correspondingly, the percentage of backcrosses showing semisterility (50% or lower hatchability) increased from 29% at 2000 r to 55% at 3000 r and 65% at 3500 r. F₁ test females showed a significantly different dose/response relationship compared with F₁ test males (p<.01). Both average hatch and percent semi-sterility were significantly different for male and female F₁'s at 2000 r and 3000 r but not at 3500 r (p<.01).

Table 1.—Backcross data involving irradiated Delhi males and a multiple marker stock, JY (homozygous for the genes for white eyes (*w*) on chromosome 1, spot abdomen (*s*) and the dominant Silver mesonotum (*Si*) on chromosome 2 and black tarsus (*blt*) on chromosome 3).

	2000 r			3000 r			3500 r		
	♀	♂	Total	♀	♂	Total	♀	♂	Total
No. F ₁ crosses made	266	318	584	101	113	214	24	30	54
No. of F ₁ crosses ^a examined	212	213	425	41	59	100	15	25	40
No. of semisterile crosses ^b	45	80	125	15	40	55	9	17	26
Average hatch (%) (All crosses ^c)	72	57	68	65	40	52	48	41	44
Percent of crosses semisterile ^b	21	37	29	36	68	55	60	68	65

a. Crosses yielding less than 50 eggs and/or hatchability of less than 10% discarded.
b. Crosses showing egg hatch of 50% or lower.
c. % hatch from control backcrosses involving unirradiated Delhi males and JY females is presented in Table 4.

Table 2 gives the translocation yield at various radiation doses. A total of forty-five translocation heterozygotes were isolated and identified by following the segregation of the markers. A higher percentage of translocations per F₁ examined were obtained at the highest dose but the fertility averages of the translocations did not significantly differ with dose. Fertility percentages of different translocations varied widely, from 11-50.

Twenty-eight translocations were induced at 2000 r, nine at 3000 r and eight at 3500 r. Twenty-two of the translocations involved chromosomes 1 and 2, eight involved chromosomes 1 and 3 and fifteen involved chromosomes 2 and 3. A G-test of independence showed that the frequencies of the various types of translocations induced were not a function of the dose. However, when the 72 translocations induced in our laboratory in both ROCK and DELHI strains were pooled according to translocation types and subjected to a G-test of independence, the number of translocation types were significantly different and the order of recovery from the most frequent to the least frequent was 1:2, 2:3, 1:3. The order of frequency of chromosomes involved in translocations was 2, 1, 3, which is neither a reflection of the physical nor the genetic length of the chromosomes. The order for the physical length from the longest to the shortest is 2, 3, 1 (McDonald and Rai 1970c) and for the genetic length is 1, 2, 3 (Craig and Hickey 1967).

At each dose there were more semi-sterile male backcrosses than female backcrosses. Thus in Table 1 at 2000 r, for example, adults had to be scored for 37% of the scorable egg papers from male F₁'s but only 21% of the papers from female F₁'s. Nevertheless, the number of translocations recovered as a percentage of the number of scorable egg papers from each sex was fairly equal at all three doses (Table 2). Thus in backcrossing males, more time is spent in scoring adults for genetic markers than when females are backcrossed, while the translocation return is the same.

Recombination Data

Crossover data for the forty-five translocations are listed in Table 3. Information was obtained for recombination between pseudolinked genes, e.g., between the loci for spot (*s*) and black tarsus (*blt*), and Silver (*Si*) and black tarsus in the case of 2:3 translocation heterozygotes, and between *sex-s*, *sex-Si*, *w-s*, *w-Si* in the case of 1:2 heterozygotes. Linkage data are also presented for genes on the same chromosome when that chromosome was involved in a translocation, i.e. white-eyes and sex on chromosome 1 in the case of 1:2 and 1:3 translocations, and Silver and spot on chromosome 2 in the case of 2:3 and 1:2 translocations. Crossover values varied significantly from translocation to translocation. However, average map distances between markers on interchanged chromosomes did not differ significantly from the map distances between the same markers on the non-irradiated

Table 2.—Translocation yield at different radiation doses

	2000 r			3000 r			3500 r		
	♀	♂	Total	♀	♂	Total	♀	♂	Total
Number of translocations	15	13	28	5	4	9	3	5	8
T(1:2)	7	5	12	1	3	4	2	4	6
T(1:3)	2	4	6	0	1	1	0	1	1
T(2:3)	6	4	10	4	0	4	1	0	1
Percent Translocation yield ^a	7	6	7	12	7	9	20	20	20
Average Hatch (%)	38	31	35	34	31	33	25	31	28

a. Percent translocation yield = $\frac{\text{number of translocations}}{\text{number of F}_1 \text{ crosses examined}} \times 100$.

Table 3.—Data on fertility, mortality, transmission and recombination of the translocation heterozygotes isolated

Translo- cation	Sex- linked	Hatch (%)	Pre-Adult Mortality (%)	Translocation ^a transmission (%)	Crossover pseudolinked				Crossover linked	
					Sex-s (%)	Sex-Si (%)	w-s (%)	w-Si (%)	Sex-w (%)	s-Si (%)
A. T(1:2) Translocation heterozygotes										
2000 r										
T(1:2)8H	m	43	72	56	— ^c	—	12	32	—	—
T(1:2)9H	m	48	38	41* ^b	13	—	29	—	18	—
T(1:2)10H	M	38	40	52	20	25	15	—	8	13
T(1:2)4L	M	30	94	44	—	15	—	—	—	—
T(1:2)5L	m	23	65	59*	—	—	19	11	—	15
T(1:2)9L	M	35	63	63	17	29	25	29	8	21
T(1:2)11L	M	11	23	60	5	5	23	23	17	0
T(1:2)12L	m	29	48	53	—	—	9	24	—	22
T(1:2)13L	m	46	91	50	—	—	0	4	—	8
T(1:2)14L	M	28	66	49	4	8	4	8	7	4
T(1:2)34H	m	36	30	58	—	—	12	4	—	—
T(1:2)35H	m	28	40	48	—	—	13	8	—	—
3000 r										
T(1:2)25H	M	23	30	50	18	10	11	6	9	8
T(1:2)26H	m	30	23	75	—	—	23	9	—	—
T(1:2)27H	M	34	40	65**	0	6	0	12	4	15
T(1:2)30H	M	22	37	54	30	15	16	23	13	17
3500 r										
T(1:2)14H	m	37	20	43	25	—	25	27	—	16
T(1:2)16H	m	21	63	73***	16	17	15	14	—	14
T(1:2)17H	M	42	43	53	15	20	22	32	20	24
T(1:2)18H	M	38	55	53	20	22	6	12	10	11
T(1:2)19H	M	45	22	70***	13	16	21	21	19	10
T(1:2)20H	M	11	13	52	0	5	8	13	9	15
B. T(1:3) Translocation heterozygotes					Sex-bl ^t (%)	w-bl ^t (%)				
T(1:3)5H	M	40	59	76***	17	25				
T(1:3)11H	M	50	10	41* ^b	10	9				
T(1:3)23H	M	18	25	67***	10	18				
T(1:3)33H	m	42	36	50	—	11				
T(1:3)6L	m	36	45	68***	—	4				
T(1:3)8L	M	13	8	62	6	13				
3000 r										
T(1:3)24H	M	45	44	55	17	9				
3500 r										
T(1:3)15H	M	18	28	54	0	6				

a. Assuming that wild-type progeny (for the pseudolinked markers) are translocation heterozygotes.

b. Indicates that translocation transmission significantly differs from the expected 50%.

(* p<0.05 ** p<0.01 *** p<0.001)

c. Dash indicates that there were less than 100 progeny produced; therefore insufficient data to determine cross-over values.

Translo- cation	Sex of translo- cated Parent	Hatch (%)	Pre-Adult Mortality (%)	Translocation ^a transmission (%)	Cross-over pseudolinked s-bl ^t Si-bl ^t (%) (%)		Cross-over linke s-Si (%)
C. T(2:3) Translocation heterozygotes							
T(2:3)6H	♀	31	17	35***	0	0	0
T(2:3)7H	♂	50	8	78***	3	7	7
T(2:3)12H	♀	50	53	64***	12	8	8
T(2:3)21H	♀	50	60	57	6	3	5
T(2:3)22H	♂	50	45	48	10	5	5
T(2:3)7L	♀	32	72	65***	20	23	24
T(2:3)10L	♀	38	28	58***	2	10	10
T(2:3)15L	♂	23	30	28***	0	2	2
T(2:3)16L	♀	39	76	50	14	9	5
T(2:3)17L	♂	25	69	49	4	37	26
3000 r							
T(2:3)28H	♀	18	57	53	6	11	12
T(2:3)29H	♀	28	61	67***	25	27	11
T(2:3)31H	♀	45	74	80***	5	6	2
T(2:3)32H	♀	49	27	63*	0	2	9
3500 r							
T(2:3)13H	♀	17	20	32	5	7	4

a. Assuming that wild-type progeny (for the pseudolinked markers) are translocation heterozygotes.

b. Indicates that translocation transmission significantly differs from the expected 50%.

(* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$)

c. Dash indicates that there were less than 100 progeny produced; therefore insufficient data to determine cross-over values.

control crosses (Table 4). The average crossover values for chromosome 1 markers were 16% for the control crosses and 15% for the experimental crosses. The average crossover values for the chromosome 2 markers were 7% for the control crosses and 11% for the experimental crosses.

Recombination data for pseudolinked genes in all translocations were examined and frequency distributions of percent recombination were constructed for all possible combinations of markers (Fig. 1A) in order to determine if breakpoints were randomly distributed or preferentially localized along the chromosome length. Crossover values involving each markers were also pooled and arranged according to frequency of classes with class intervals at every five percent (Fig. 1B). An analysis of variance of pooled pseudolinkage recombination data showed the data for the five markers to be significantly different from each other ($p < .05$). The recombination frequency for pseudolinkage between the chromosome 3 marker, *blt*, and the other four markers on chromosomes 1 and 2 was significantly lower than any other combination ($p < .01$), suggesting preferential breakage near the *blt* locus.

Pre-adult Mortality

Pre-adult mortality figures are recorded in Tables 3, 4 and 5. An analysis of variance of pre-adult mortality compared the three groups of translocations obtained and the two series of control crosses, one irradiated at 2000 r but not carrying any translocations and one non-irradiated. The overall F-statistic was highly significant ($p < .001$) as was the F-test comparing the translocated with the non-translocated crosses ($p < .01$). Comparisons among the three translocation groups and

Number of Individuals

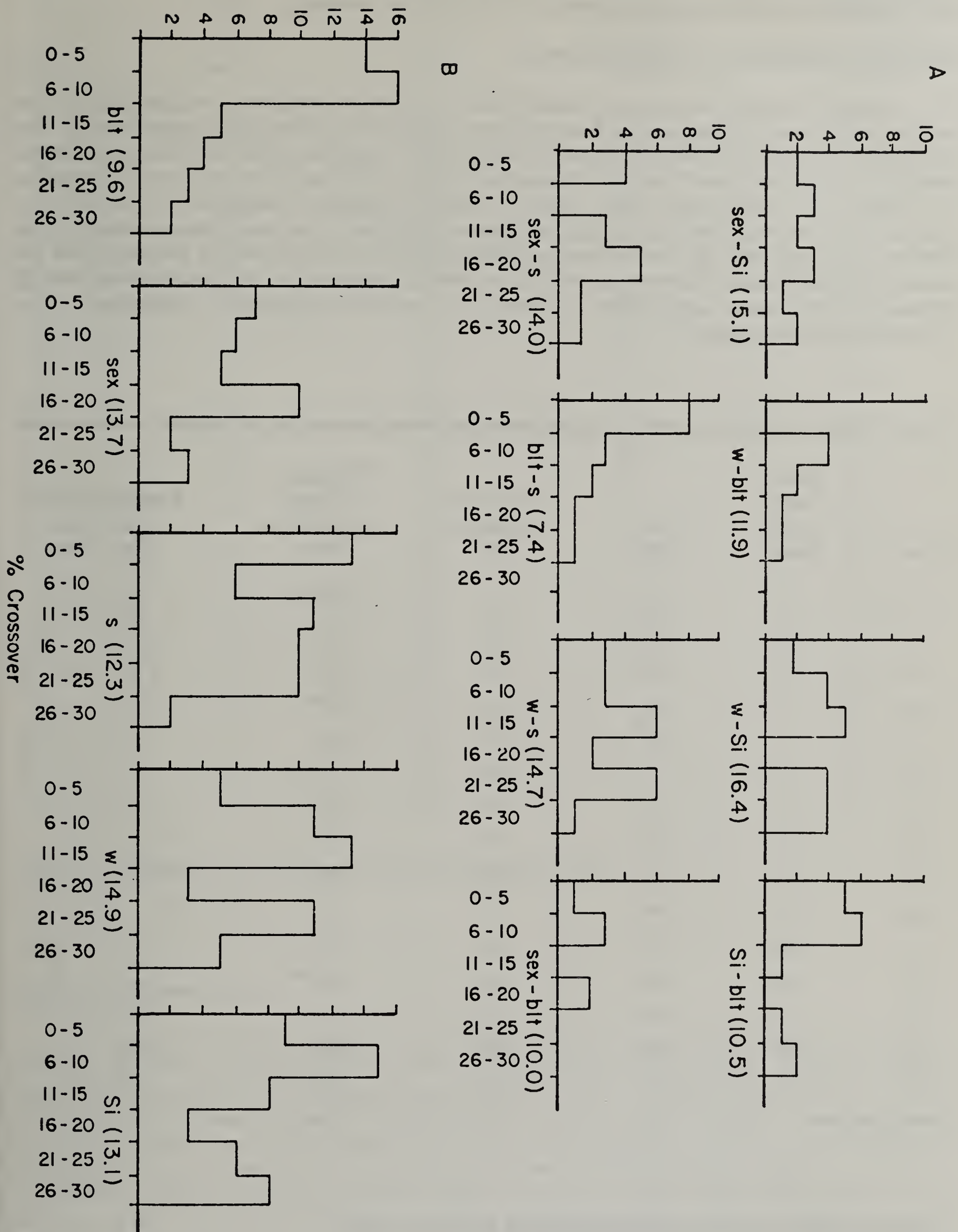


Fig. 1.—Frequency distributions of crossover data for pseudolinked markers (A) and the values pooled for each marker (B). Numbers in parenthesis indicate mean recombination.

also between the irradiated and the non-irradiated groups were not significant. Thus the relatively high pre-adult mortality associated with several translocations appeared to be a function of the chromosomal rearrangement and independent of the radiation treatment.

Preferential Transmission of Wild-type Markers

Crosses between translocation heterozygotes carrying the wild-type markers and mutant marked individuals with the standard karyotype were expected to produce equal proportions (1:1) of translocated wild-type, and non-translocated mutant progeny. Eighteen of the forty-five translocations deviated in both directions from this expectation (Table 3). In five of the twenty-nine irradiated, non-translocated control crosses, higher than the expected frequency of transmission of the wild-type markers were observed (Table 5). Similar deviation was exhibited by the nonirradiated control crosses (Table 4). In some cases the transmission percentage deviated from 50% but the sample size was too small to yield significance. However, an analysis of variance comparing the translocations and controls showed no significance among them, indicating that variable transmission is independent of the chromosomal rearrangement.

Table 4.—Data on fertility, mortality, transmission and recombination for unirradiated control crosses

Cross	Sex of back- cross Parent	Hatch (%)	Pre-Adult Mortality (%)	Wild-type marker transmission (%)	Cross-over linked	
					Sex-w (%)	s-Si (%)
1	♂	85	8	70***a	12	11
2	♂	90	10	61*	14	6
3	♂	93	8	54	10	12
4	♀	95	19	59*	— ^b	2
5	♀	88	33	58	—	6
6	♀	77	59	72***	—	—
7	♀	93	11	58	—	5
8	♀	96	5	55	—	14
9	♀	97	43	47	—	6
10	♀	99	0	53	—	5
11	♀	95	55	56	—	6
12	♀	97	56	68***	—	4
13	♂	97	0	63	17	9
14	♂	92	56	40	33	4
15	♂	74	19	66*	8	3
Average values		91	25	59	16	7

a. Indicates wild-type marker transmission significantly different from 50%

(* p<0.5, *** p<.001).

b. Dash indicates that there were less than 100 progeny produced; therefore insufficient data to determine cross-over values.

Table 5.—Data on fertility, mortality, transmission and recombination for irradiated control crosses

Cross	Sex of back- cross parent	Hatch (%)	Pre-Adult Mortality (%)	Wild-type marker transmission (%)
1	♂	37	26	53
2	♀	53	21	46
3	♂	34	0	43
4	♂	52	20	40
5	♂	52	28	65*a
6	♀	48	18	57
7	♂	10	0	50
8	♂	27	44	67*
9	♂	45	20	52
10	♀	32	18	47
11	♀	51	19	52
12	♂	35	25	48
13	♂	70	9	55
14	♀	47	48	63
15	♀	43	46	60
16	♀	47	—	57
17	♀	49	8	59
18	♀	47	28	61*
19	♀	36	6	57
20	♀	57	5	53
21	♀	90	24	74***
22	♀	70	22	55
23	♂	45	11	64*
24	♂	53	—	53
25	♂	25	8	50
26	♂	26	25	59
27	♀	35	15	54
28	♀	59	—	59

a. Indicates wild-type marker transmission significantly different from 50%

(* p<.05, *** p<.001)

Translocation Homozygotes

All of the 45 translocations induced in the Delhi stock were tested for homozygosity. Of these, only two, T(1:3)6L and T(2:3)12H, were viable as homozygotes. Five single pair matings of possible translocation homozygotes of the former type T(1:3)6L and 11 matings of the latter T(2:3)12H produced only wild-type progeny indicating that at least one of the parents in each cross was homozygous for the translocation being tested. Two of these T(1:3)6L lines and 7 of the T(2:3)12H lines again produced no mutant-marked progeny after several generations of inbreeding. In addition, a two-generation test cross with the multiple marker stock after a period of inbreeding resulted in no mutant progeny for the first generation, and the second generation progeny with pseudolinked markers in both the homozygotes. This revealed that the translocations were still present in the lines and that the founding single pairs were translocation homozygotes. Presence of homomorphic chromosome pairs at metaphase-I in primary spermatocytes of males and at somatic metaphases in oogonial cells in females provided cytological confirmation of translocation homozygosity in both stocks.

Discussion

There was a marked difference in fertility between male and female offspring of males irradiated to produce translocations. Males showed significantly higher average sterility than females. Irradiated males transmitted a treated chromosome 1 with the female-determining allele, m , to their daughters and a treated chromosome 1 with the male-determining allele, M , to their sons. Seemingly, the only difference between the two chromosomes was the sex locus, although there has been some indication from previous linkage studies that the sex-determining segment may comprise a portion of chromosome 1 as long as six units (Craig and Hickey 1967). In any case, our data suggest that the M -bearing chromosome is more radio sensitive than the m bearing. A similar sex differential was reported from *Aedes aegypti*-*Aedes mascarensis* hybridization studies (Hartberg and Craig 1968).

An analysis of recombination data showed that individual map distances between linked markers on interchanged chromosomes were variable but their average did not differ significantly from map distances between the same markers in the non-irradiated control crosses. While a wide range in crossover values is not unusual for this species (Craig and Hickey 1967), it is possible that individual translocations do affect crossing over. The testing of this possibility requires larger numbers of individuals than were obtained in this study. On examination of 3:4 translocations in *Drosophila melanogaster*, Dobzhansky (1929) found variations in map distances between linked genes according to where the breakpoint was located on that chromosome.

Average recombination between linked genes on non-translocated chromosomes (last column in tables 3 and 4) was also not significantly different from the control. However, this may again be a result of pooling since Hinton's (1965) work with *D. melanogaster* revealed interchromosomal effects of autosomal translocations on the X chromosome which were a function of the length of the interstitial distances of the interchanges.

An analysis of the recombination data for pseudolinked genes revealed that values rarely exceeded 30%. Backcrosses which showed greater than 30% recombination between two markers were seldom scored as translocations. Consequently, a translocation would be recovered if one of its breakpoints occurred fifteen map units on either side of a marker on the other chromosome (Fig. 2a). A translocation would also be detected if one breakpoint occurred within this fifteen map unit limit on one chromosome and within fifteen to thirty map units away from a marker on a second chromosome. Translocations would be lost, however, in which both breakpoints occurred in the regions of fifteen to thirty map units from the markers. This resolution would allow for the isolation of translocations from a total map length of 203 units. A schematic representation of the present linkage map is presented in Fig. 2b. The average chiasma frequency for this species is 5 per primary spermatocyte (Rai, unpublished); so it is probable that the present map of 107 genetic units is an underestimation of the actual genetic length. The total known linkage map for this species using our control data is only 100 units. The possible surveyable length using the five-marker stock was adjusted to the actual locations of the markers on their respective chromosomes (Fig. 2c). Eighteen

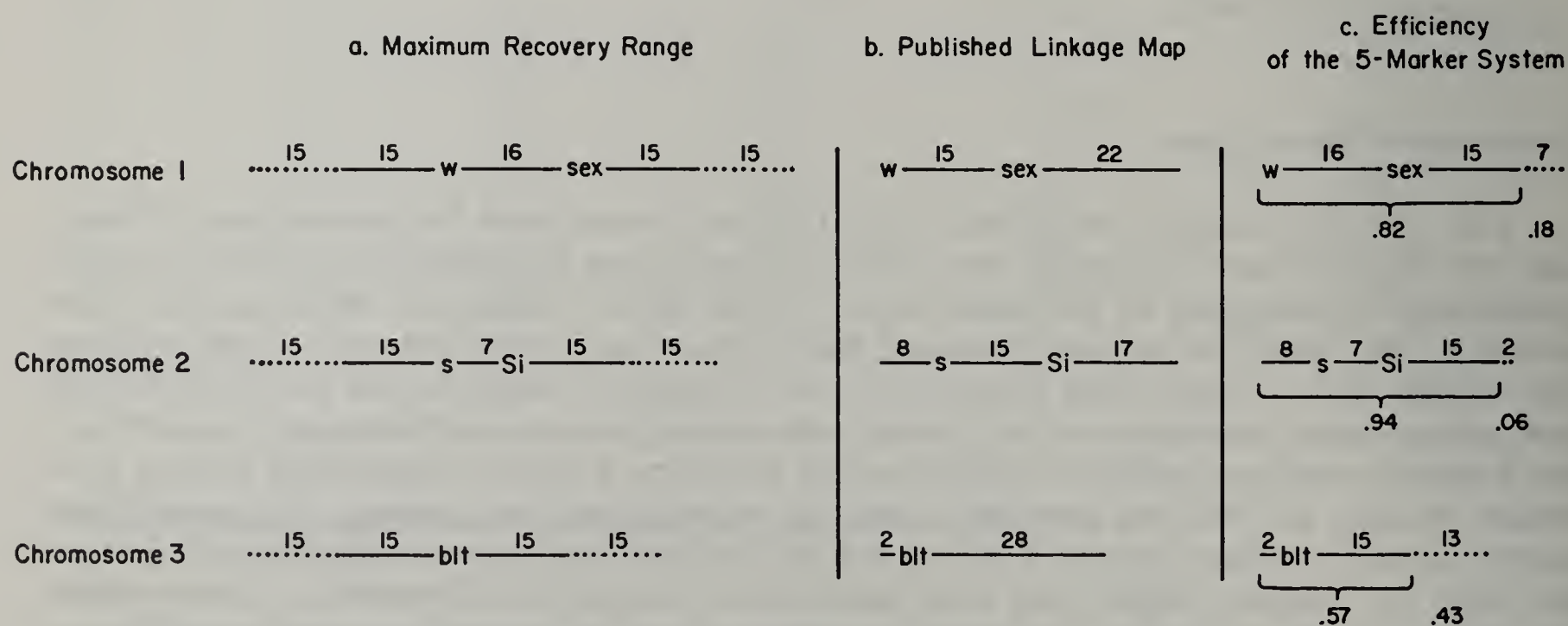


Fig. 2.—Estimated length of the linkage map surveyed. Translocations were recovered if one or both breakpoints occurred in the area represented by solid lines in a and b. Translocations were “lost” if both breakpoints were located in the dotted line segments. The published linkage map is from Craig and Hickey (1967).

percent of chromosome 1, 6% of chromosome 2 and 43% of chromosome 3 are more than fifteen map units away from the markers used for the crosses. Since translocations were not recovered in which both breakpoints occurred in these regions, .01 (.18 x .06) of the 1:2 translocations, .08 (.18 x .43) of the 1:3 translocations, and .03 (.06 x .43) of the 2:3 translocations, or .12 of the total translocations would be lost. The reciprocal value, .88, is the measure of efficiency of the five-marker system for surveying the *A. aegypti* genome for induced translocations. An efficiency rate of 88% (of all translocations induced, 88% could be recovered) is probably an overestimation since the actual genetic length of each chromosome is yet to be determined.

One of the most interesting conclusions that emerged from analysis of the recombination data was that the distribution of radiation-induced breakage on chromosome 3 was non-random. After x-irradiation of human lymphocytes, Caspersson et al. (1972) noted differences in radiation sensitivity between chromosomes and also within chromosomes. Similarly, Jancey and Walden (1972) analyzed the distribution of breakpoints in the chromosomes of *Zea mays* and *D. melanogaster* and found greater than expected frequencies of breakage in regions near the centromere and, in the case of maize, actually in the centromere. The pooled crossover values for pseudolinked markers in our translocations revealed significantly lower recombination involving *blt* when compared to the other four markers, indicating a clustering of breakpoints near this locus. McDonald and Rai (1970c) showed that *blt* in *A. aegypti* is located close to the nucleolus organizing region on the long arm of chromosome 3. After treatment with radiomimetic compounds, Kihlman (1963) also noted that breaks in chromosomes of root tips of *Vicia faba* were localized as high as 95.2% in the nucleolar constriction. It is probable that the nucleolus organizing region in this species, as in *V. faba*, is particularly susceptible to breakage.

Despite the proposed usefulness of translocation homozygotes in population control programs, they have been difficult to obtain in all vector species in which they have been sought (Laven et al. 1971, Curtis et al. 1972, Wagoner et al. 1969, Sakai et al. 1971, Childress, 1969, Rai et al. 1970). Only 2.1% (8/383) of the heterozygotes induced in vector species have been rendered homozygous. Non-viability of the homozygotes may result from the original radiation damage, tolerable in the heterozygous state but lethal when homozygous (Lorimer et al. 1972). Both homozygotes recovered from this screening were isolated from the mosquitoes irradiated at the lowest of the three doses.

This work with the forty-five translocations in the DELHI stock suggests that position effect may be playing an important role. Pre-adult mortality was found to be not a function of radiation dose used but rather of the particular chromosome rearrangement. Translocated lines had a much higher mortality than did the controls ($p < .01$). If disruption of the normal linear order of the genome is serious enough to affect the development of heterozygous individuals adversely, it is not surprising that homozygous individuals are seldom recovered.

Several release strategies with the four translocation homozygotes now available in *A. aegypti* are being considered for population control and/or replacement. Double translocation heterozygotes which are formed by crossing two different homozygotes and/or single heterozygotes have been synthesized for various combinations and the level of their fertility ascertained for the two and three chromosome double translocation heterozygotes (Rai et al. 1974). In addition, the sex-distorter gene which modifies sex ratio in favor of males (Craig and Hickey 1967) has been linked with the two sex-linked translocation homozygotes at the WHO/ICMR Research Unit in Delhi (Curtis, personal communication). Field releases of the integrated double translocation heterozygote — sex-ratio distorter stock were conducted in Sonapat, a large urban town near Delhi. Field releases were also conducted at the coastal station of the International Center of Insect Physiology and Ecology in Mombasa, Kenya utilizing some of these same translocation stocks. The emphasis of the field work in Delhi was on evaluating genetic control and in Mombasa on population replacement.

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Current Status of Genetic Control of the Australian Sheep Blowfly, *Lucilia Cuprina* (Wiedemann) (Diptera: Calliphoridae)

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Introduction

Lucilia cuprina (Wied.) occurs throughout the sheep grazing regions of Australia (Waterhouse 1962), as well as outside these areas in the subtropical and tropical zones, and coastal New South Wales. Its status as the major myiasis pest of sheep in Australia has been recognized for several decades (Mackerras and Fuller 1937). A recent survey in southeastern Australia found *L. cuprina* larvae in 89% of all myiasis which contained a single species (J.E. Watts, personal communication). In 1969-70, the latest season for which figures are available, the losses to the sheep industry attributed to blowflies were estimated at \$28 million (Bureau of Agricultural Economics 1972). Allowing for recent changes in cost indices and sheep numbers (J.M. Malecky, personal communication), a reasonable estimate for 1974-5 would probably be close to \$41 million. Past attempts at biological control, current practices in farm management and insecticidal methods have failed to reduce *L. cuprina* numbers or their effects to economically insignificant levels (Foster and Whitten 1974, Foster et al. 1975, for reviews).

Because of the failure of traditional methods, autocidal means of controlling this species are being considered. The conventional sterile insect release method (SIRM), i.e., the regular release of radiosterilized adult flies of both sexes, would not be economically feasible (Waterhouse 1962). For example, we estimate that to rear and release 1000 sterile flies/wk/km² for 40 wk over the 3.5 million km² of sheep country in Australia (Fig. 1) would cost \$30-40 million per year, of which more than two-thirds would be distribution costs. By concentrating on the wheat-sheep and high rainfall zones (Fig. 1) which comprise only half the sheep country, but contain 77% of the sheep and sustain 74% of the total losses (Bureau of Agricultural Economics 1972), the cost: potential benefit ratio could be lowered to approximately 1:2. However, even this reduction in cost is unlikely to be considered acceptable. Consequently we have concentrated our efforts on developing cheaper modifications of, as well as possible alternatives to, SIRM.

Since 1971 a concerted study of the genetics and ecology of *L. cuprina* has been under way (Foster and Whitten 1974, Foster et al. 1975, Whitten et al. 1975, for reviews). The genetic work has mainly been aimed at the synthesis of chromosomally rearranged strains for release. Ecological studies have been directed towards developing reliable methods for measuring the size and dynamics of *L. cuprina* populations, as an aid both to determining control strategy and to the assessment of field trials. In addition, several small-scale field trials involving the release of genetically marked males (Whitten et al. 1973) or irradiation-sterilized adults or pupae (unpublished data from two trials) have established that laboratory-reared *L. cuprina* males are reasonably competitive for mating purposes with wild flies in the field. These encouraging results and the successful synthesis of compound chromosome (CC) strains in *L. cuprina* (Foster et al. 1976) have allowed us to shift the emphasis of the project, from the mainly theoretical, towards a closer examination of the practical problems we are likely to encounter in implementing a program of genetic control.

AUSTRALIAN SHEEP ZONES



Fig. 1. – Australian sheep industry climatic zones (after Bureau of Agricultural Economics, 1972).

Compound Chromosomes

The synthesis of a CC strain is possibly the most significant step towards reduction in the cost of genetic control to an acceptable level. One possibility would be that if a wild population could be replaced with a CC strain and the population fertility thereby reduced to an extent where economic benefits occur, long-term control might be achieved at the cost of only a few (e.g., 5-10) releases, compared with the 40 or so releases per year likely to be required by SIRM. In addition to the potential sterility effects, the presence of the CC strain should retard re-establishment of wild flies in an area (if appropriate geographical boundaries are chosen), since occasional immigrants should be at a frequency disadvantage in having only incompatible CC flies with which to mate. Moreover, with CC or other genetically semisterile strains, the possibility of releasing insects at immature stages rather than as adults should result in large savings in rearing and distribution costs. We have recently completed field trials which indicate that free-falling mature third instar larvae of a translocation strain dropped from aircraft survive to adulthood and compete well with wild flies for mates (unpublished data). Release of *L. cuprina* as larvae would eliminate the cost of the drop-boxes necessary for adult flies (approximately \$75 per million flies) and should reduce distribution costs several fold, since many more larvae than adults can be carried in an aircraft.

Although the use of CC strains in the manner suggested above may result in effective control of *L. cuprina*, the possibilities must be considered that after a replacement of the wild population in an area: (1) the CC strain may not be fertile enough to maintain a population and so eventually die out; or (2) the strain may be so fertile that there is little if any reduction of the pest problem. Alternative (1) would be quite acceptable on islands and in areas where reinvasion by wild *L. cuprina* is not likely to occur, but not in the majority of mainland Australia. Alternative (2) could be handled in several

different ways, one of which would be to replace the wild strain with two or more mutually incompatible CC strains simultaneously, resulting in a greater population sterility and providing effective control for perhaps 5-7 generations (Foster and Whitten 1974). This would require releases of one or more CC strains for a short period every year or so, to maintain equal populations of the different CC strains and therefore high levels of sterility. Another solution to alternative (2) which, although perhaps more costly, may prove easier to manage (*cf.* Curtis and Hill 1971), would be to control the CC strain by SIRM. This would presumably be easier than controlling a wild strain by SIRM, since suppression of the less fertile CC strain should require the release of fewer sterile males.

Female Killing System

There would be considerable advantages to a SIRM-type program if a practical scheme could be devised for eliminating females, before or during the early stage of the final mass-rearing operation. We have pursued this objective in *L. cuprina* by linking a conditional lethal mutation, in this case susceptibility to the insecticide dieldrin, to sex (Whitten and Foster 1975). By selecting translocations between the male-determining Y chromosome and a chromosome 5 carrying the gene for dieldrin resistance, *Rdl* (Whitten et al. 1975), we have established strains in which dieldrin resistance is holandrically inherited. By dipping newly hatched (1-4 hr old) larvae of such a strain in a dieldrin solution, females are killed and males can be reared to maturity (unpublished data). In three field trials adult males from the strain *T(Y;5)Rdl* survived and competed well with wild males, after being dipped in dieldrin solution as first instar larvae and dropped from aircraft as third instars (unpublished data). Thus the prospects for development of a practical female-killing system for use in mass-rearing of *L. cuprina* are very encouraging. One of the problems yet to be solved before the method will be applicable to large numbers of larvae (several millions at a time) is that a high degree of synchrony of egg hatch appears to be required for a good separation of the sexes. Eggs that hatch after the dipping procedure produce larvae that are little if at all affected by the dieldrin, and older larvae present at the time of dipping may be less sensitive to the discriminating dose of dieldrin effective for 1-4 hr old larvae. At present we are experimenting with methods of synchronizing egg hatch, as well as administration of the insecticide in the larval diet, which would remove the need for synchrony. It is possible that a similar scheme using the allele for resistance to organophosphorus-insecticides, *Rop-lic*, (Arnold and Whitten 1976) or a combination of *Rdl* and *Rop* will ultimately prove more efficacious for developing a female-killing system.

Visible Mutants as Conditional Lethals

Until we can demonstrate with confidence that CC strains will provide a practical means of controlling *L. cuprina*, it is desirable to pursue alternative means of genetic control which can be used either to complement CC strains or as an entirely separate form of control. One of the weaknesses of the 'CC strain' strategies is that they require both sexes of the released insect to compete effectively with their field counterparts. Furthermore, general application of CC strains to other pest species is limited by the inherent difficulties in developing such strains. With this in mind we set out to establish a genetic system of control that demanded the simplest genetics for construction of suitable strains and which entailed minimal assumptions for its successful implementation.

A series of eye colour mutants which had been isolated in *L. cuprina* for conventional genetic mapping experiments and which could be made readily available in other important pest species was selected. Each of four autosomes carries at least one recessive mutation affecting eye pigmentation (Whitten et al. 1975): chromosome 3, *white* (*w*); 4, *tangerine* (*tg*); 5, *topaz* (*to*) and 6, *yellow* (*y*). The order of epistasis for these loci is $w > y > to > tg$ such that in the presence of *w/w*, the other mutants are not expressed (unpublished data), i.e., the stock *w/w;to/to;y/y* appears white-eyed. Some of the eye colour mutants have other pleiotropic effects which impinge on fitness, but, in the presence of *w/w*, these effects are suppressed. Under laboratory conditions white-eyed flies appear to be able to function normally and present no difficulties for mass-rearing. However in the field we have established that white and topaz-eyed flies are not trappable (unpublished data) and we interpret this information to mean that such flies are not capable of performing some essential function. Thus eye colour mutants of the class we have described above can be considered as conditional lethals, the conditions for lethality being satisfied under field, but not laboratory, conditions.

By irradiating a wild type strain of *L. cuprina* it has been possible to induce a series of reciprocal translocations between the Y chromosome and various autosomes which limit expression of these eye colour mutants to the female sex. Thus the true breeding strain $w/w \text{ } \text{♀} \times T(Y;3)w^+/w \text{ } \text{♂}$ has wild type males whereas all the females are white-eyed. Similarly $w/w;to/to \text{ } \text{♀} \times T(Y;3;5)w^+;to^+/w;to \text{ } \text{♂}$ produces all wild type males and white-eyed females. If the males we irradiate are homozygous for resistance to dieldrin, i.e., are *Rdl/Rdl*, then a $T(Y;3;5)$ strain, in these circumstances, would be described as $w/w;to/to \text{ } \text{♀} \times T(Y;3;5)Rdl \text{ } w^+;to^+/Rdl^+w;to \text{ } \text{♂}$. In such a strain the males, in addition to being wild type for eye colour, would carry one dose of the resistance gene for dieldrin, while all the females would be susceptible to dieldrin and have white eyes. It should be noted that these females are cytologically normal and therefore they should be fully fertile under laboratory conditions. The object of incorporating *Rdl* into the translocations is to retain the option of eliminating these females from the mass-rearing program for those reasons outlined above. However, it should be appreciated that the release of these females into the field should have no impact whatsoever on the field populations, but that their elimination before the mass-rearing operation would reduce the cost of mass-rearing and distribution.

If we assume that it is possible to swamp the natural population by a release of males carrying Y-autosome translocations and heterozygous for a set of eye colour mutants and to retain such a release ratio for at least two generations, then it might be possible to achieve levels of genetic death as summarized in Table 1. For comparison, the levels of genetic death are given both under laboratory and field conditions. The former is important to know because it indicates the difficulties we would encounter in mass-rearing such a strain. The latter of course gives an optimum measure of the efficacy of the strategy under field conditions. Two attractive features of the scheme are the level of flexibility we have in determining the degree of sterility we can set for our mass-rearing strain and, secondly, that there is differential mortality between the two sexes in the field. In fact the level of genetic death amongst females, which for many pest species is likely to be the critical sex in determining the reproductive capacity of a population, can be increased to very much higher levels than that obtained for males. Not only are female zygotes eliminated in such circumstances because of aneuploidy arising from the chromosome rearrangements, but they also incur a segregational load following homozygosis of the different eye colour mutants in generations following the release. Earlier field trials, where males bearing Y-autosome translocations were released from aircraft as mature third instar larvae, suggested that such males are competitive (unpublished data). We propose to release similar males during the 1976/7 field season, but incorporating the eye mutants as described in this section.

Release Strategy

Generally speaking, the optimal time to initiate a program of genetic control is when population densities are low or declining. In the case of *L. cuprina* the patterns of adult fly

Table 1.—Estimated levels of genetic death under laboratory and field conditions in Y-autosome translocation strains carrying female-limited eye colour mutations.

Cross	Genetic Death ^a	
	Laboratory	Field
$to/+ \times T(Y;5)to$	30%	65%
$to/+;w/+ \times T(Y;5;3)to,w$	70%	92.5%
$to/+;w/+;y/+ \times T(Y;5;3;6)/to,w;y$	80%	97.5%

a. % kill of female zygotes of given cross; figures for laboratory genetic death are based on experience with translocation strains of *L. cuprina*.

abundance recorded over several years have shown that, in the cool and temperate regions of Australia, low densities occur predictably only during late autumn, winter and early spring, although occasionally numbers are low during dry summers (Fig. 2).

To investigate the population dynamics of overwintering of *L. cuprina* and to obtain information relevant to possible release strategies during the autumn-spring period, fully-fed third instar larvae of a laboratory strain were released into field cages at Canberra during the autumn to spring period of 1973. The results (Fig. 3) suggest that flies developing from larvae released in midwinter (late July-early August) will emerge at the same time as overwintering larvae, but may not suffer such heavy mortality. These results also suggest that by regular releases starting in midwinter, it should be possible to achieve a much higher released:native ratio during the critical spring months (October-November) than would be possible with releases commencing in the spring. The peculiar pattern of late emergence of the Sept. 10 release (Fig. 3) is difficult to understand, although it may have been related to an unusually heavy rainfall (42.9 mm) two days after the release. Similar studies of overwintering larvae of both field and laboratory strains are continuing at several sites.

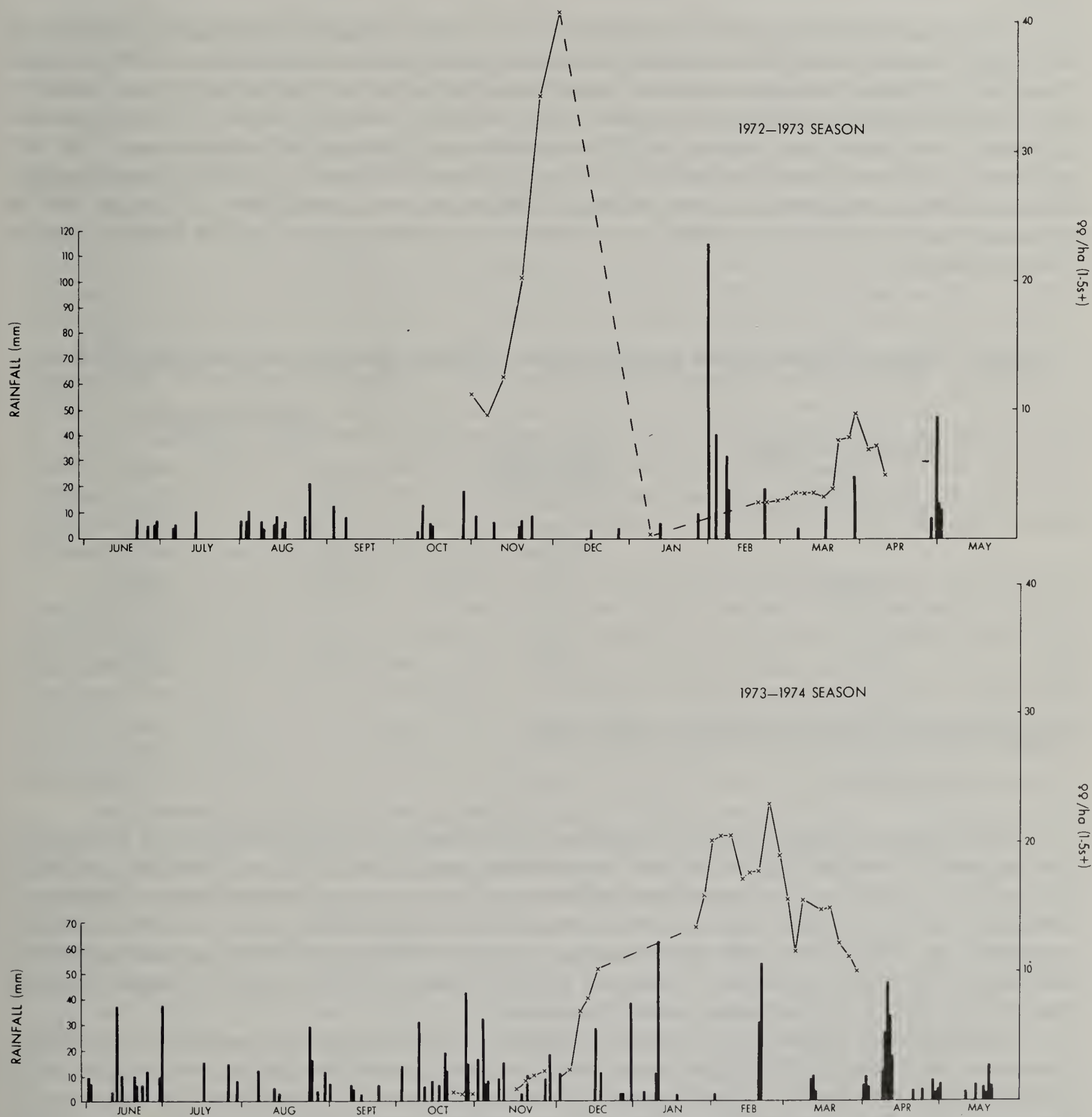


Fig. 2. — Population estimates of female *L. cuprina* (x — x) and associated rainfall distribution (bar graphs) at Murrumbateman, N.S.W. Only females that had matured at least one batch of eggs are included in the estimates. Points are not shown when one standard error exceeded the value of that point. Registrations of rainfall that did not exceed 2 mm are not shown. (a) 1972-73 season, (b) 1973-74 season.

Besides the obvious economic criteria for evaluating a control program, it is also important for us to be able to evaluate preliminary trials using ecological criteria. Since our genetic control measures are designed to reduce the reproductive potential of field populations, we need to be able to measure the reproductive state and size of the populations concerned. Consequently, considerable effort has been devoted to studying the dynamics of field populations.

Information concerning the reproductive state of *L. cuprina* populations can be obtained by determining the stage of ovarian development of samples of field-caught females (Vogt et al. 1974). Briefly, females develop eggs in batches of 100-300 and may produce several batches, although the mean number of ovarian cycles per field female is generally less than one. Resources such as protein and suitable oviposition sites must be available for a female to complete the ovarian cycle, so the reproductive age structure of a field sample can be used to infer environmental factors which may affect a population's reproductive capacity. For a more comprehensive review, see Foster et al. (1975).

The presence or absence of *L. cuprina* in an area can be established easily since adult flies can be readily obtained from the field using liver-baited traps (Vogt and Havenstein 1974). A crude indication of relative abundance can be obtained from the number of flies caught per trap; however, the number of flies trapped as such does not yield sufficiently accurate estimates of density for our purposes, since the sex ratio and age structure of adults caught in traps differ from those of the field population. This is evidenced by the fact that marked flies of different sex and age released together and recaptured on the same day show markedly different recovery rates (Table 2). Thus, in order to estimate densities of adults in the field, the density of each sex and age class (for females) must be treated separately.

Table 2.—Recovery rates of three groups of flies of different ages captured on the day of release.

Reproductive stage of ♀*	Day degree equivalents	Recovery Rates†	
		♂	♀
I	30	6.1	4.4
II-IV	39	5.6	3.6
V	61+	2.6	3.5

† Expressed as (the number caught/number released) x 100

* See Vogt et al., (1974).

The density estimates obtained during the 1972-73 and 1973-74 seasons (Fig. 2) are based on the recapture of marked flies of various reproductive ages (Jolly 1965) and therefore contain an unknown bias. In order to minimize this bias due to differences in age structure between marked and unmarked flies, only field-caught flies were marked and released. The bias is further reduced by presenting the estimates as three-point moving averages. Although the above procedures provide reasonably good approximations to the actual field densities, the effort required to mark individual flies precludes its use for evaluating control programs.

Large number of flies can be marked effectively by allowing them to emerge through coloured fluorescent dust (Norris 1957). By releasing wild-type flies of known sex and age, each marked with a different dust, the recovery rates (proportion recaptured) can be determined for each sex and age-class on any day. Since wild females can be sorted into corresponding classes (Vogt et al. 1974), the number trapped in each class can be converted to a density estimate. Unfortunately, this procedure is not suitable for evaluating control programs, since the release of fully fertile female flies would tend to defeat the purpose of genetic control.

In addition to the different recovery rates of different age and sex classes, the number of flies caught during a trapping period is influenced by weather factors such as rainfall, air temperature, incoming solar radiation and wind velocity. If the relationships between these factors and trappability are determined for each age and sex class, it should be possible to adjust trap catch numbers and age structures to allow for changes in recovery rates due to different weather conditions. Thus trap catches could be converted directly into density estimates without the need to release marked flies.

This approach is being followed in attempts to develop a low-cost method of monitoring the overall fitness of the released flies under field conditions and their impact on the rate of increase of wild fly numbers. During the 1975-76 fly season, releases of marked flies in different sex and age classes were made at fortnightly intervals to standardize their recovery rates against varying weather conditions. Analysis of the data is now in progress and the results will be presented elsewhere.

Population Dynamics

Field densities of *L. cuprina* appear to be strongly influenced by weather conditions, which affect rates of development, survival and the availability of resources. Figure 2 shows the variations in density during the 1972-73 and 1973-74 fly seasons at Murrumbateman, New South Wales. These two seasons differed markedly in their patterns of adult density. The initial population level in the spring of 1972 was approximately 10-fold greater than in 1973. Excessively wet conditions in the winter and spring of 1973 (Fig. 2) may have reduced the survival of overwintering larvae in that year. On the other hand, wet conditions in summer appeared to favour an increase in *L. cuprina* population density. In the 1972-73 season, spring was followed by a summer drought and the population density declined from ca. 40 females/ha at the beginning of December to less than 1 female/ha at the beginning of January. Following heavy falls of rain in February 1973 the population again increased. No such dry spell occurred in 1973-74, nor was there a marked mid-summer trough in fly numbers.

Although relevant field data are difficult to obtain, we may reasonably relate these wet/dry fluctuations in numbers to changes in the availability of essential resources such as protein for vitellogenesis, or susceptible sheep as oviposition sites (Tyndale-Biscoe and Kitching 1974, Foster et al. 1975). Generally, sheep tend to become more susceptible to myiasis during wet conditions. This is partly because flushes of new growth in pastures, associated with rainfall, tend to raise the level of helminth infestation in sheep which causes fecal scouring and thus predisposes the breech area to flystrike (Morely et al. 1976). Further, prolonged wetness induces bacterial development in fleece (fleece rot) which may predispose sheep to fly attack.

Another aspect of population dynamics which has an important bearing on control strategy, is the rate of movement of the fly. At Murrumbateman, N.S.W., an area of predominantly improved pastures and high stocking rates, dispersal estimates based on the recovery of marked flies indicate that distances travelled are relatively small. In summer, when activity is highest, the mean flight distances recorded 17 days after release were 2.8 km and 2.2 km for males and females, respectively. In both cases, there was a tendency for the released flies to disperse upwind. The Murrumbateman area may be considered a favourable one from the point of view of resource availability, so that the low mobility recorded there may not be representative of fly movement in poorer areas.

An interesting example of how population age structures may provide clues to field behaviour arises out of a marked difference between the age structure of the fly population at Murrumbateman and the one 30 km away at Sutton, which is an area of unimproved pastures, low stocking rates and generally less fertile soil. The proportion of gravid flies was consistently much higher at Sutton than at Murrumbateman (unpublished data). This is probably due, at least partly, to the lower availability of oviposition sites at Sutton. However, it also appears unlikely that many of the gravid females at Sutton originated there, since the ratio of flies in their first ovarian cycle to those in their second cycle was similar at the two study sites, whereas it should have been much higher at Sutton if locally-reared flies were responsible for the build-up. The most likely explanation appears to be that the high proportion of gravid flies at Sutton reflects net displacement of gravid flies into that area from adjacent, more favourable, breeding sites. This interpretation is supported by laboratory and field studies of age-specific activity (unpublished data), which indicate that gravid females are more active than other age classes. If indeed this interpretation is correct, it implies that rate of movement is not greatly influenced by resource availability and that the dispersal rates observed at Murrumbateman may apply to other areas as well.

In order to assess the fitness of the CC strain, several field and field-cage experiments were performed during the 1975-76 season. At the time of these releases the only wild type¹ CC strain available was a highly inbred one with an entirely laboratory-based genetic background, *C(5L)2,+;C(5R)1,+* (Foster et al. 1976). Initially, this strain had an average egg to adult survival of 6%, which, combined with inefficient mass rearing methods, presented severe problems in obtaining enough insects to release, as well as maintain breeding stocks. However, after 6 months (i.e., 9 laboratory generations), the egg to adult survival had increased to 12% and rearing methods had improved to the point where in February, 1976, we were able to rear 1 million larvae per batch, starting with 80,000 adult females.

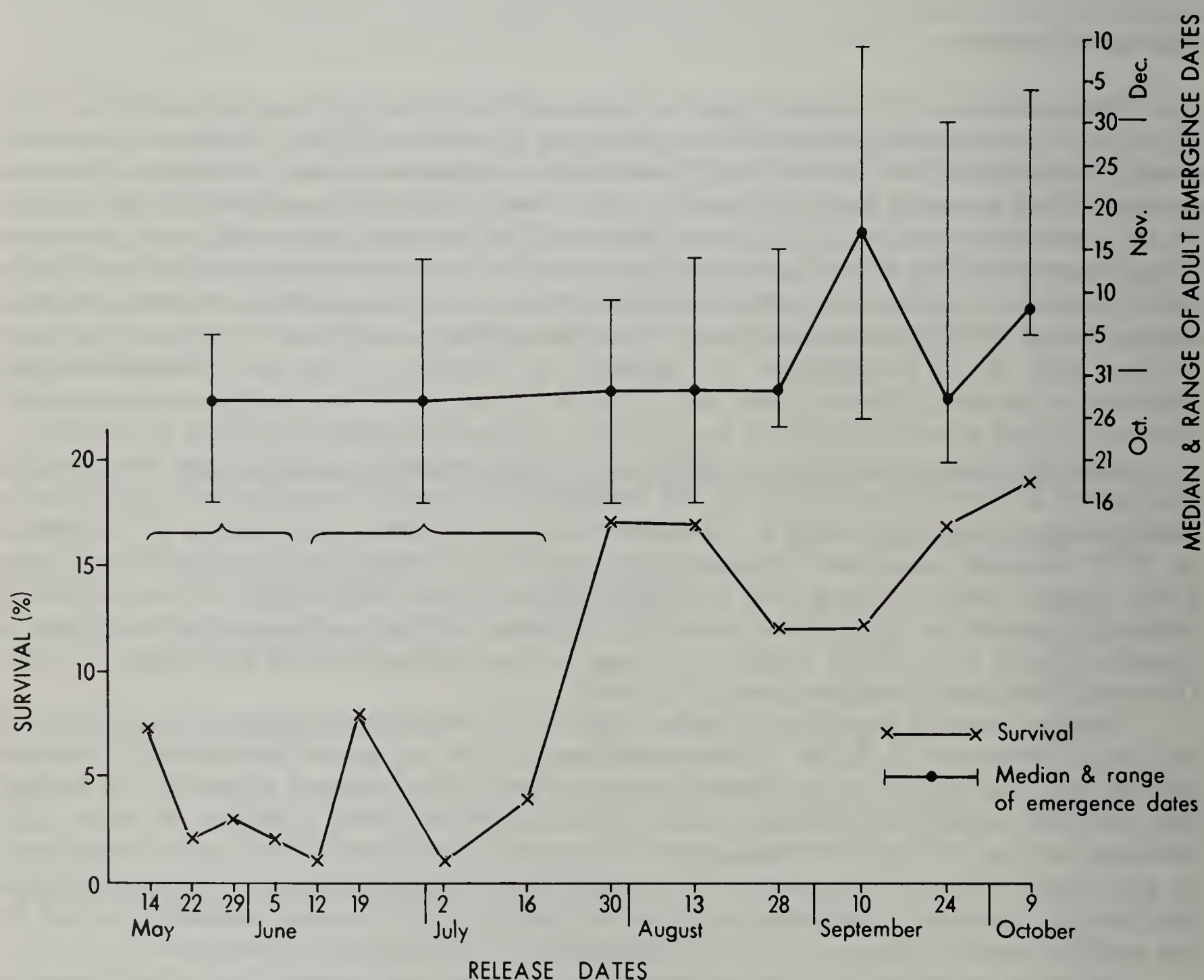


Fig. 3.—Survival and adult emergence dates of larvae released into field cages at Canberra between May and October, 1973.

The first trials involved releasing adults marked with a fluorescent dust in the centre of a trapping grid and determining their subsequent dispersal and trappability. Dispersal of the CC strain was comparable to that of a field strain for the week following the release (unpublished data). Trappability of CC♂♂ was comparable to other strains (Table 3), suggesting that CC ♂♂ survived well during this period. CC ♀♀ were markedly less trappable (Table 3). Analysis of daily recapture ratios of

¹ Although adults were all wild type, approx. 13% of individuals in this strain were homozygous for the chromosome 2 mutation *black pupa* (*bp*).

Table 3.—Trappability of released *L. cuprina* strains* one week after release.

	<u>Field-F₁</u>	<u>Lab</u>	<u>$\frac{to\ w}{+ ; +}$</u>	<u>Compound</u>
♂♂	13.9%†	7.9%	12.9%	8.4%
♀♀	16.5%	10.8%	10.2%	3.3%

* Strain origins are as follows:

Field-F₁ = first generation progeny of field-inseminated ♀♀ trapped at Murrumbateman.

Lab = a laboratory colony derived from field-inseminated ♀♀ trapped near Canberra approx. 1 year before the present release.

$to/+;w/+$ = wild-type progeny of the laboratory backcross $to/to;w/w$ ♀ x $to/+;w/+$ ♂ (see text).

Compound = the laboratory compound chromosome strain $C(5L)2,+;C(5R)1,+$ (see text).

† (number of flies trapped / number released) x 100.

the four strains (unpublished data) suggests that (i) CC ♀♀ were initially less trappable (approx. 1/3 — 1/2 than the other ♀♀, and (ii) on the fifth day after the release the recapture rate of CC ♀♀ dropped by half relative to the other strains, and remained constant for the rest of the trapping period. These results suggest that the CC ♀♀ were less fit than normal ♀♀.

The second trial involved releasing mature $C(5L)2,+;C(5R)1,+$ larvae from aircraft over a 300 km² area surrounding the trapping grid. Releases were made weekly at the rate of 1000 larvae/km² for the first 3 weeks and 2000/km² for the next 5 weeks, after which releases ceased. Recovery of adults from larvae released onto the ground in a field cage at the same time as the start of the aerial releases, was 47%, which compares favourably with survival of wild type larvae in field cages (Foster et al. 1975). However, recovery as adults of larvae released from the air proved to be much more difficult. Of several hundred trapped ♂♂ which were progeny tested, none were CC, although this may have been due to differential mortality of CC and wild ♂♂ in traps (typically, mortality of *L. cuprina* ♂♂ in traps is high, sometimes exceeding 90%). Tests of field-inseminated ♀♀ produced similarly discouraging results for the first 4 weeks, but from week 5 onward there was some evidence of matings involving CC flies in the field (Table 4). These data suggest that, although both sexes are able to mate in the field, the CC strain has a low mating competitiveness. Based on previous trials with $T(Y;5)Rdl$ ♂♂ (unpublished data) we would have expected approx. 5-10% of field ♀♀ to be mated by CC ♂♂ if the latter were competitive.

There are several possible reasons for the poor performance of the CC strain in the field. Firstly, the narrowness of the genetic base of the strain could be responsible, particularly as only a few individuals were used to found the strain. In addition, the marked change in fertility of the CC strain in colony cages suggests that severe selection may have occurred in the strain. Secondly, mass rearing methods could have contributed to the poor fitness of the CC strains. Thirdly, technical problems associated with handling of the mature larvae may have affected their fitness. This could have been important in the present case, since an incubator in which larvae were held prior to release was later found to be malfunctioning. A program to broaden the genetic base of the CC strain by introducing field genetic material (Foster et al. 1972) is under way and mass rearing and handling procedures are under constant review.

1976/7 Season and Beyond

The disappointing results of the 1975/6 field trials using a CC strain have forced upon us a series of investigations which are now in progress. Many of these have been alluded to in the text above and are not discussed further.

The 1976/7 season has amongst its objectives (1) an expansion of the mass rearing facility to a capability of 2-5 million flies per week and (2) the production and release of the translocation strain $to;w$ x $T(Y;5;3)to^+;w^+/to;w$ as mature third instar larvae. A progenitor of this strain was released in 1974/5 and appeared competitive under field conditions (unpublished data). Laboratory cage experiments in which males of the $T(Y;5;3)$ strain compete with wild type males are currently

indicating that this new translocation strain actually has a competitive advantage over its wild type counterpart. Releases of some 2-5 million T(Y;5;3) flies per week are planned for 2 sites near Canberra. Data will be collected on (1) the frequency of T(Y;5;3) males in the field, (2) percentage of females inseminated by these males, (3) frequency attained by the 2 eye colour mutants *w* and *to* during the release period and their decline after releases end, (4) genetic loads achieved during the release period and its decay after releases cease, and (5) ecological data on fly numbers and strike incidence within and outside the release zones over the period.

Subsequent activities will clearly depend on the outcome of these trials and on progress made in the intervening time to produce a competitive compound strain of *L. cuprina*.

Table 4.—Results of progeny tests of field-inseminated ♀♀ trapped at Murrumbateman during compound chromosome release trial.

Week	Wild ♀ x Wild ♂	Wild ♀ x CC ♂	CC ♀ x CC ♂
		<i>or</i> CC ♀ x wild ♂	
1	27	0	0
2	100	0	0
3	104	0	0
4	160	0	0
5	217	1	0
6	132	0	1
7	194	3	0
8	165	1	0
9	89	0	0

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Isozyme Variability Studies of Translocation Homozygotes in the House Fly, *Musca domestica* L.

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ABSTRACT

A survey of eight polymorphic isozyme loci in homozygous translocation bearing strains of the house fly, *Musca domestica* L., revealed that each strain was genetically unique when compared with the other strains or with two strains originating directly from the field. Gene fixation, gene frequency alterations at loci retaining polymorphisms observed in the wild samples, and alterations in the frequency of heterozygotes vs. homozygotes all contributed to the genetic structuring of the translocation stocks. The results suggest the genetic indeterminacy of translocation stocks originating from the genetic base provided by a single fertile mating and indicate that given strains will have to be tested individually for their fitness characteristics in field situations.

We have initiated a program at the USDA Metabolism and Radiation Research Laboratory (MRRL) in Fargo, North Dakota, to investigate isozymes of the house fly, *Musca domestica* L., as an integral part of the genetic control research effort with this species. Isozymes are multiple molecular forms of enzymes that have at least one common substrate. They are coded for genetically by structural genes and, based primarily on their charge characteristics under given sets of conditions, they can be separated on a support medium using electrophoretic methods and subsequently visualized by histochemical staining techniques. The advantage of the process is that the biochemical products of individual genes can be visualized and scored in a straightforward manner on electrophoretic gels. Moreover, crude extracts of individual insects can be examined for a number of variant enzyme systems.

Isozymes may be allelic or nonallelic; where they represent an allelic series they are termed allozymes. We have concentrated primarily on working with allozymes because once the genetics of allozymic forms are described it is possible to monitor variability at given loci in individuals or among individuals in populations. Fortunately, the genes of most allozyme series are codominant in that their products can be distinguished in heterozygous individuals.

To date, we have characterized the genetics of six different enzymatic systems exhibiting allozymic variability at one or more loci in *M. domestica* (Narang et al. 1976, McDonald et al. 1975, McDonald et al., unpublished data), and we have initiated a number of studies utilizing the various alleles of these systems as genetic markers. One such study has involved a variability survey of our homozygous translocation bearing strains, (T/T) in comparison with samples taken directly from two different field populations, (+/+). All translocation strains at the MRRL originated from the progeny of single females; the strains are reared continuously on a standard medium under set environmental conditions. The purpose of the survey was to examine the possible genetic effects of the translocation recovery procedure and subsequent rearing conditions on the translocation stocks.

Materials and Methods

House Fly Strains

All T/T strains (Table 1) were originally isolated in the heterozygous condition b- the technique of Wagoner (1967) and were subsequently made homozygous by appropriate crossing procedures. Strains 2, 3, 4, and 7 carry an inversion in the long arm of chromosome 3 (McDonald and Overland 1973a). Also, strain 5 possesses a recessive heat-sensitive lethal mutation closely linked with the translocated 3rd chromosome (McDonald and Overland 1973b). All the T/T stocks have been maintained in the laboratory for 3-5 years.

The +/+ samples were obtained by sweeping for wild flies at two different locations in the vicinity of Fargo, North Dakota on two occasions covering a period of 2 weeks during the spring of 1976.

Table 1.—Isozyme variability of T/T and +/+ strains of the house fly, *Musca domestica* L.

Strain number	Translocated chromosomes	Enzymatic Loci ¹							
		To2	Odhl	Hk2	Ak2	Pgm1	Pgm2	Est1	Est2
1	1;2	1.0 ²	1.0 ²	.05,.95	.04,.96	1.0 ¹	1.0 ¹	1.0 ^N	+
2	3;5	1.0 ²	1.0 ²	.33,.67	.30,.70	.04 ² ,.96 ⁵	1.0 ¹	+	+
3	3;5	1.0 ²	1.0 ²	.37,.63	.35,.65	1.0 ⁵	.83,.17	+	+
4	3;5	1.0 ²	1.0 ²	.04,.96	.04,.96	.42 ² ,.58 ⁵	.46,.54	+	+
5	3;5	1.0 ²	1.0 ²	.42,.58	no data	.54 ² ,.46 ⁵	1.0 ¹	1.0 ^N	1.0 ^C
6	4;5	1.0 ²	1.0 ²	.38,.62	.37,.63	1.0 ²	.21,.79	+	+
7	2;3;5	1.0 ²	1.0 ²	.33,.67	.21,.79	.25 ² ,.75 ²	1.0 ¹	+	+
8	2;4;5	1.0 ²	1.0 ²	.04,.96	.04,.96	1.0 ²	1.0 ¹	+	+
9	2;4;5	1.0 ²	1.0 ²	.25,.75	.21,.79	1.0 ²	1.0 ¹	+	+
W ¹		.12,.88	.04,.76,.20	.52,.48	.38,.62	.03,.21, .16,.39,.21	.97,.03	+	+
W ²		.03,.97	0.0,.82,.18	.36,.64	.36,.64	.02,.18, .26,.26,.28	.97,.03	+	+

¹Superscripts denote allele designations. All other values show frequencies of alleles in order of decreasing mobility in acrylamide gels. Sample sizes vary from 12-60 genomes.

Sample Preparation and Electrophoresis

Sample preparation was described earlier (McDonald et al. 1975). Vertical polyacrylamide gel electrophoresis was performed in glass analytical electrophoretic cells using 5.0 and 6.5% separating gels and a tris-glycine buffer system. All runs were conducted at 5°C with 35 ma constant current until a bromophenol blue tracing dye had traveled ca. 60 nm into the separating gel.

Enzyme Systems and Staining Techniques

The polymorphic enzyme systems surveyed were as follows: Octanol dehydrogenase (*Odhl*), Tetrazolium oxidase (*To2*), Hexokinase (*Hk2*), Adenylate kinase (*Ak2*), Phosphoglucumutase (*Pgml* and *Pgm2*), and Esterase (*Estl* and *Est2*). The inheritance patterns and staining methods for *Odh*, *To*, and *Est* were reported previously (McDonald et al. 1975, Narang et al. 1976). The techniques employed with *Hk*, *Ak* and *Pgm* will be described in another report along with the genetics.

Results

Gene Frequency Comparisons

Gene frequencies for the loci examined are reported in Table 1. Three variability patterns were noted among the loci studied when the T/T stocks were compared with the +/+ samples (W^1 and W^2 of Tables 1 and 2). In the first pattern, the most common wild type alleles of *To2* and *Odhl* were fixed in all of the T/T stocks examined (Table 1, columns 3 and 4). In direct contrast, all T/T strains were polymorphic at the *Hk2* and *Ak2* loci although gene frequency differences existed among the various aberrant stocks and between given T/T strains and the +/+ samples. Of interest is the fact that gene frequencies approximately paralleled each other for the fast and slow alleles of *Hk2* and *Ak2* in all but two of the populations tested (T/T strain 7 and +/+ strain W^1); also, the fastest migrating allozyme of these two systems was almost always the rarer of the two alternate forms present.

Table 2.—Comparison of allozyme frequencies and the frequencies of heterozygotes vs. homozygotes in T/T and +/+ fly strains.

number	Translocated chromosomes	Gene Frequencies				Frequency of het./hom.			
		Hk2	Ak2	Pgm1	Pgm2	Hk2	Ak2	Pgm1	Pgm2
1	1;2	.05,.95	.04,.96	*	*	.18/.82	.08/.92	*	*
2	3;5	.33,.67	.30,.70	.04 ² ,.96 ⁵	*	.50/.50	.38/.67	.08/.92	*
3	3;5	.37,.63	.35,.65	*	.83,.17	.75/.25	.70/.30	*	.33/.67
4	3;5	.04,.96	.04,.96	.42 ² ,.58 ⁵	.46,.54	.08/.92	.08/.92	.92/.08	.92/.08
5	3;5	.42,.58	no data	.54 ² ,.46 ⁵	*	.83/.17	no data	.58/.42	*
6	4;5	.38,.62	.37,.63	*	.21,.79	.75/.25	.25/.75	*	.25/.75
7	2;3;5	.33,.67	.21,.79	.25 ² ,.75 ⁵	*	.67/.33	.42/.58	.33/.67	*
8	2;4;5	.04,.96	.04,.96	*	*	.10/.90	.10/.90	*	*
9	2;4;5	.25,.75	.21,.79	*	*	.50/.50	.42/.58	*	*
W^1		.52,.48	.38,.62	.03,.21, .16,.39,.21	.97,.03	.42/.58	.38/.62	.60/.40	.06/.94
W^2		.36,.64	.36,.64	.02,.18, .26,.26,.28	.97,.03	.50/.50	.38/.62	.71/.29	.06/.94

*Asterisk indicates no variability at indicated loci. Gene frequency values given in order of decreasing mobility in acrylamide gels. Superscripts denote allele designations where given.

An intermediate pattern of variability was observed at each of the two *Pgm* and *Est* loci. Five *Pgm1* alleles were recorded from the +/+ populations (Table 1, column 7). However, a single *Pgm1* gene was fixed in five of the T/T strains even though the allele present was not always the same. The other four strains were polymorphic at the *Pgm1* locus, but possessed only two of the forms (*Pgm1*² and *Pgm1*⁵) detected in the +/+ populations. Also, gene frequency differences were observed among the T/T strains polymorphic at *Pgm1*. Finally, T/T strain 1 was homozygous for *Pgm1*¹ and represented the only interchange stock possessing an allele other than *Pgm1*² or *Pgm1*⁵; the *Pgm1*¹ gene was the rarest allele recorded from the wild samples.

The most common *Pgm2* allele of the +/+ strains was fixed in six of the translocation bearing stocks. However, three T/T stocks retained the rare *Pgm2*² form, and in two of these *Pgm2*² was present in greater frequency than the more common *Pgm2*¹ allele of the field samples (Table 1, column 8).

Codominant and null alleles (Narang et al. 1976) were detected at both the *Est1* and *Est2* loci in the +/+ populations, and seven of the nine T/T strains retained the polymorphisms. However, null alleles (produce no band when homozygous) were fixed at the *Est1* locus in T/T strains 1 and 5; also,

a codominant allele was fixed at *Est2* in strain 5 (Table 1, columns 9 and 10). Actual gene frequencies were not recorded for the *Est1* and *Est2* loci because we could not determine whether individuals exhibiting single bands were heterozygous for null alleles.

Heterozygote Frequencies

The frequencies of heterozygotes vs. homozygotes at the *Hk2*, *Ak2*, *Pgm1* and *Pgm2* loci provided a second measure of variability. Theoretically, the genetic framework of a population could diver even though gene frequencies were similar as shown in the following example:

Pop. No.	Population Genotypes*				Gene Frequencies	Heterozygote Frequency
	1	2	3	4		
1	a/a	a/a	a ¹ /a ¹	a ¹ /a ¹	a=0.5, a ¹ =0.5	0.0
2	a/a ¹	a/a ¹	a/a ¹	a/a ¹	a=0.5, a ¹ =0.5	1.0
3	a/a	a/a ¹	a/a ¹	a ¹ /a ¹	a=0.5, a ¹ =0.5	0.5

*a and a¹ denote alternate alleles at a given locus.

The test results are shown in Table 2 and indicate definite differences in overall genetic architecture when the T/T populations are compared among themselves or with their wild counterparts. Heterozygosity at given loci was low in some populations owing to the rarity of one of the alternate allozymes (see *Hk2* and *Ak2* for strains 1, 4, and 8, for example). However, at higher levels of allozyme variability, differences in heterozygosity could be distinguished among strains possessing similar gene frequencies at both the *Hk2* and *Ak2* loci (see strains 2, 3, and 7, for example). Also, differences in the frequency of heterozygotes were readily apparent at both *Pgm1* and *Pgm2* in those T/T strains exhibiting polymorphism (see strains 4 and 5 for *Pgm1*, for example.)

Six of the T/T stocks showed levels of heterozygosity equal to or greater than that of their wild counterparts at the *Hk2* locus. The level of heterozygosity at *Ak2* more closely paralleled that of the +/+ populations in strains exhibiting about the same gene frequencies. However, heterozygosity in strain 3 was nearly double that recorded for either +/+ population. The *Pgm2* locus showed strikingly higher levels of heterozygosity than the +/+ flies in those T/T strains retaining the polymorphism (see strains 3, 4, and 6); however, the rarity of the fast allele in *Pgm2* samples from the field could account for this disparity. Finally, the results with *Pgm1* were mixed with the level of T/T heterozygosity being either above or below that of the wild strains.

Discussion

There can be little doubt that each house fly T/T stock surveyed during the study was genetically different from the other T/T stocks or from the +/+ samples with regard to the enzyme systems examined. At least three processes contributed to the genetic structuring of the various aberrant strains. First, there was a loss of variability at some loci, and in many cases gene fixation had occurred. The reduced variability may have resulted from the original translocation isolation procedure (by chance) or could have occurred because of drift or selection against allelic alternatives within T/T strains subsequent to their isolation. At present, we cannot distinguish the relative roles of the two alternate processes in the strains examined because all of the T/T stocks had been maintained in the laboratory for several years prior to the study. Secondly, some loci retained the polymorphisms observed in the +/+ samples, but gene frequency alternations were evident among various strains. Presumably, the T/T stocks had had time to reach equilibrium at these loci though the frequency of some alleles was quite low in given strains and fixation of the more common form may eventually occur because of genetic drift. Finally, changes in the frequencies of heterozygotes were recorded among strains; in some instances these changes distinguished strains having similar gene frequencies at a particular polymorphic locus.

The results indicate that, in addition to losses in variability, a major problem inherent in the development of genetic control programs against house flies will be the genetic indeterminacy of engineered strains. There are presently no studies that directly correlate information recorded from isozyme studies to specific fitness or behavioral traits although Bush (1976) has suggested a relationship between selection for flight muscle enzymes and the fitness of screwworm flies (*Cochliomyia hominivorax* (Coquerel)) employed in the Southwest Screwworm Eradication Program. Moreover, there is a growing body of evidence that many allozyme variants have adaptive significance, particularly with regard to the formation of ecotypes (see McKechnie et al. 1975, Johnson 1976, for examples). The inference is that losses of variability, relative allozyme frequency differences, and differences in heterozygosity/homozygosity frequencies between genetic control stocks and their wild counterparts may combine to make genetic control strains noncompetitive when they are placed in field situations. Gene variability may be partially re-established by the intermating of strains. However, the arrangement of genetic material in the released strains may be equally important to field survival, particularly when portions of genomes must pass through a number of generations to achieve suppression, as with chromosome aberrations. To date, this aspect of population control genetics has been largely overlooked.

In closing, we should note that with many insects (there may be exceptions) the problem of securing appropriate genetic material in genetically altered strains will be quite different from that of retaining genetic material in strains brought into the laboratory for biological or sterile-male insect control programs. In the former instance the control strains must usually survive on the genetic base provided by a single fertile mating, and various strains may reach different genetic endpoints even when they originate from the same source and undergo identical rearing regimens. In this regard such strains are highly illustrative of Mayr's Founder Principle (1963). Strains brought into the laboratory for biological or sterile-male programs may likewise be subject to founder effects depending on how representative the sample is with respect to field variability. However, there is some evidence to support the idea that strains from representative samples will exhibit less among-strain variance when subjected to similar rearing regimens than nonrepresentative samples (Dobzhansky and Pavlovsky 1957). Also, it may be possible to achieve better competitiveness with such strains by programming environmental variables into the rearing process to maintain variability (Long 1970, Powell 1971, Wistrand and Powell 1976). Modulating the rearing environment would be much less effective with genetically altered strains because they may differ from the wild-type to begin with, in terms of the amount and the arrangement of the variability. It might be possible to restore some measure of variability to interchange strains by backcrossing procedures (Whitten 1971). However, these procedures involve the production of semi-sterile heterozygotes and quite often recombination may be severely limited in those portions of the genome involved in the interchange (see Roberts 1970). Moreover, one is eventually faced with the problem of re-isolating the interchange homozygote.

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The Application of Compound Autosomes to Insect Control Including the First Experimental Successes With Compound-Fragment Combinations

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ABSTRACT

A genetic insect control technique involving population replacement by chromosomal rearrangements and population elimination using conditional lethality is reviewed. Population replacement using compound autosomes has been tested extensively under laboratory and field conditions. A new technique for replacement involving compound-fragment combinations is proposed and the results of the first cage experiments with this method are presented. The findings indicate that compound-fragment combinations are at least as effective as compounds alone in displacing standard arrangements in cages. Fitness component data suggest that compound-fragments may in fact be more effective than compounds, making them the most potent tool for genetic control presently available.

In the years since Knipling (1955) conceived the idea of sterilizing insects and then releasing them as a means of controlling their native counterparts, there have been a number of demonstrations of the successful application of the sterile insect technique. The most notable demonstration was the eradication of the screwworm, *Cochliomyia hominivorax* (Coquerel), in the southern United States and northern Mexico (Knipling 1967, Bushland 1971). During the same period other groups endeavoured to develop more sophisticated genetic methods of pest control using some of the known properties of chromosome behavior. Genetic techniques such as cytoplasmic incompatibility, hybrid sterility, inherited sterility and population replacement represent an encouraging array of insect control methods that spell an optimistic future for alternatives to conventional chemical procedures (for a recent review of genetic insect control see Fitz-Earle 1976).

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Population Replacement

The concept of replacing an entire population of pest insects having standard chromosomes with another population carrying rearranged chromosomes, which may in turn act as vectors for factors desirable from man's viewpoint, was recognized only recently (Curtis 1968, reviving and extending the work of Serebrovskii 1940, Whitten 1971). When insects homozygous for certain chromosomal rearrangements are crossed with those carrying chromosomes of standard sequence, there is reduction in viability of the hybrid progeny compared either with the rearrangement or with the standard strain. By adjusting the proportions of the two types according to their relative viability, it is possible to achieve an equilibrium, albeit an unstable one. If, however, the proportion of the rearrangement were increased, the population would be pushed in favor of the rearrangement over a few generations (Li 1955). In the context of insect control this principle of 'overflooding' could be used against target native standard populations with relative rapidity, dependent upon the difference in fitness of the two strains and their relative initial frequencies.

Conditional Lethality

Population replacement through genetic manipulations, though in itself not constituting a means for control, provides the mechanism for introducing controlling factors into native strains, since the rearranged chromosomes can serve as carriers of desirable mutations. Decisions on the types of mutations employed, should be based on ecological and economical considerations. For example, the eradication of certain classes of insects, may lead to serious ecological repercussions. In these instances the introduction of a mutation that renders the population innocuous but does not reduce the population size would be desirable. One possibility might be to introduce into a strain of disease vectors a gene for refractoriness to the disease by associating the mutant with a chromosome rearrangement. If such insects were released in sufficient numbers into an infective population, then with time the level of disease would be sharply reduced but the numbers of insects would remain relatively fixed. By contrast, the elimination of introduced insect pests of crops or livestock would be ecologically acceptable and economically desirable. Strains bearing conditional lethal mutations, which permit survival under one set of circumstances but cause death under another, would seem to be ideally suited for programs of elimination. One simple example of a conditional lethal mutation that could have application in control programs is the temperature-sensitive conditional lethal in which the insects would survive at permissive temperatures (e.g., at 22°C or below) but would die at restrictive temperatures (e.g., above 22°C). Strains carrying temperature-sensitive conditional lethal genes can be generated in the laboratory with little difficulty and currently exist in such insects as the housefly, *Musca domestica* (L.) (McDonald and Overland 1972), the wasp, *Habrobracon serinopae* (Ashmead) (Smith 1971) and the vinegar fly, *Drosophila melanogaster* (Meigen) (Suzuki et al. 1976). An increase in temperature into the restrictive zone can precipitate lethality at the egg, larval, pupal or adult stages of the life cycle depending on the mutant strain. In order to eliminate a pest population the technique would be to perform replacement at permissive temperatures (early in the season for example) of the native standard population by stocks carrying temperature-sensitive conditional lethal genes in association with chromosomal rearrangements. After successful replacement and when temperatures had risen to exceed the restrictive level of the mutant, death would begin to occur and ultimately the whole population would be eliminated. The combined principles of population replacement followed by population eradication have been applied with success under laboratory conditions using the vinegar fly (Fitz-Earle and Suzuki 1975). At present a number of international groups are actively pursuing the control of pest species using the strategy of population replacement with chromosome rearrangements and subsequent elimination by conditional lethality.

Compound Autosomes

One class of rearrangements for population replacement, which has been given much consideration in recent times, is referred to as the compound autosome. These chromosomal rearrangements differ from standard chromosomes (Fig. 1a) in that their homologous arms are attached to common centromeres rather than to different centromeres (Fig. 1b). Compound autosomes were generated first in *D. melanogaster* by E.B. Lewis and his co-workers (Rasmussen

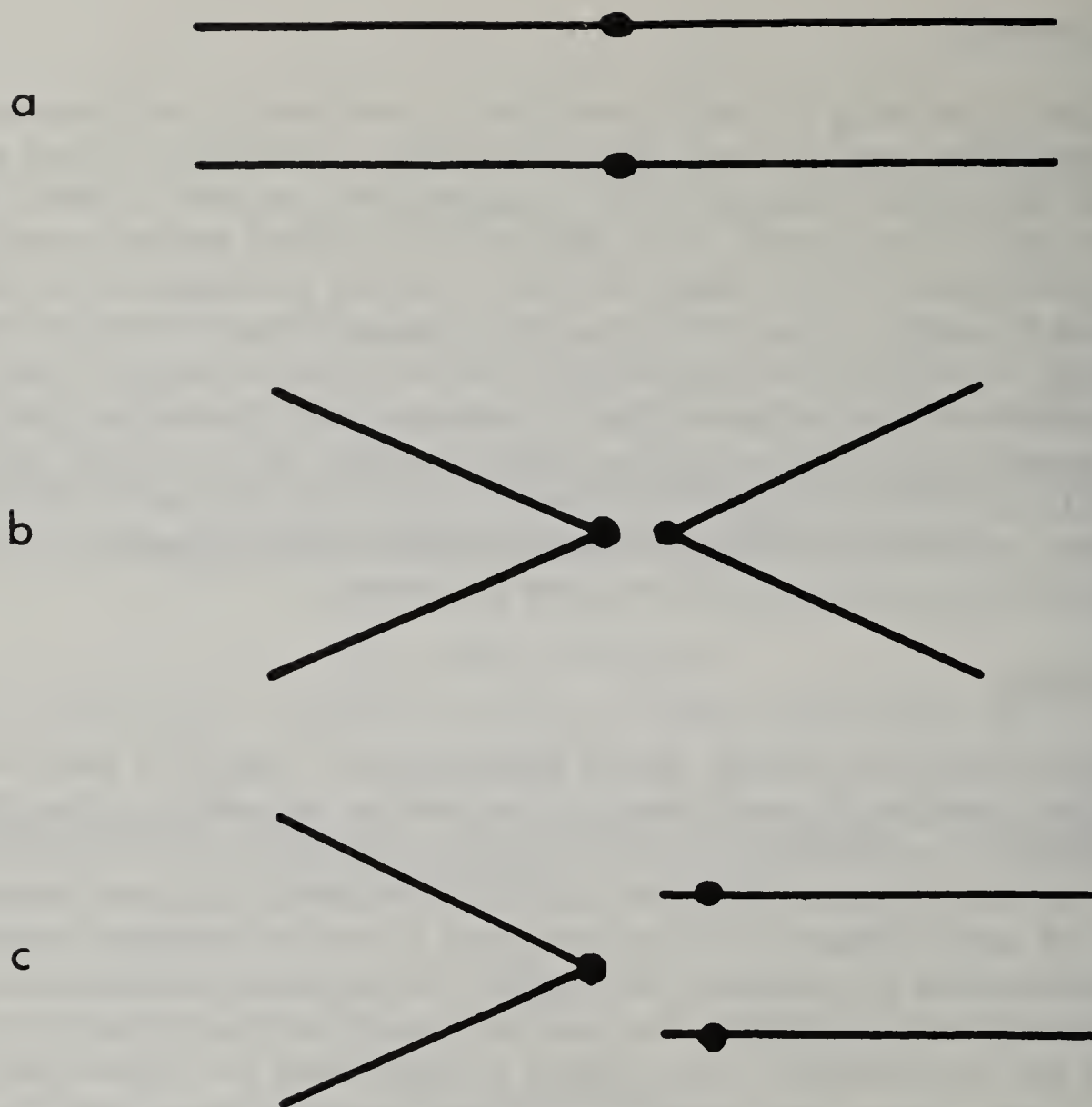


Fig. 1. —a. Standard chromosome arrangement; b. Compound left and compound right ('compound'); c. Compound left and fragment right ('fragment').

1960). The meiotic behavior of compound autosomes (hereinafter called 'compounds') in *D. melanogaster* is such that the frequency of viable zygotes is usually 25% that of the viability in a strain bearing standard chromosomes (termed 'standards') (Fig. 2), but those surviving individuals from the compound strain are perfectly competitive (for a recent review of compound autosomes in *D. melanogaster* see Holm 1976). The unique feature of compound strains, however, is that there is complete genetic isolation between them and standard strains (Fig. 3) — the ultimate reduction of viability. As a consequence, in a mixed population of compounds and standards, there would be intrastain fertility but complete interstrain sterility. The optimum condition for the principle described above therefore obtains. At this juncture, compounds have been generated widely in *D. melanogaster*, as well as recently in the sheep blowfly, *Lucilia cuprina* (Wiedemann) (Foster et al. 1976). Compounds are also being sought in other insects of economic and hygienic significance, though there is no assurance, as too with *L. cuprina*, that their meiotic behavior will parallel that of *D. melanogaster*.

Studies of competitions between compounds and standards of the vinegar fly have been conducted in the laboratory and in the field under a variety of regimes. Compounds have been shown to displace standards over discrete generations in bottles (Foster et al. 1972) and in population cages (Childress 1972, McKenzie 1976). A situation that more accurately approaches that found in the wild involves cage populations with overlapping generations and, under such circumstances, compounds have successfully replaced standards (Fitz-Earle et al. 1973, Cantelo and Childress 1975). Not surprisingly, much variability exists in the replacement capability of compound strains, but in cages established even in the ratio of 4 compounds to 1 standard (the theoretical equilibrium in terms of relative viability), and maintained over continuous generations, compounds have become fixed (Fitz-Earle 1975). Compound lines generated in strains of vinegar flies brought from the wild have also been found to be successful in displacing laboratory standards in laboratory cages at the initial ratio of 4:1 (Fitz-Earle et al. 1975). It is of interest to note that when the same native compounds were competed in cages against essentially native standards the minimum successful ratio was 5:1 compounds to standards (Fitz-Earle et al. 1975). However, laboratory-derived compounds failed to

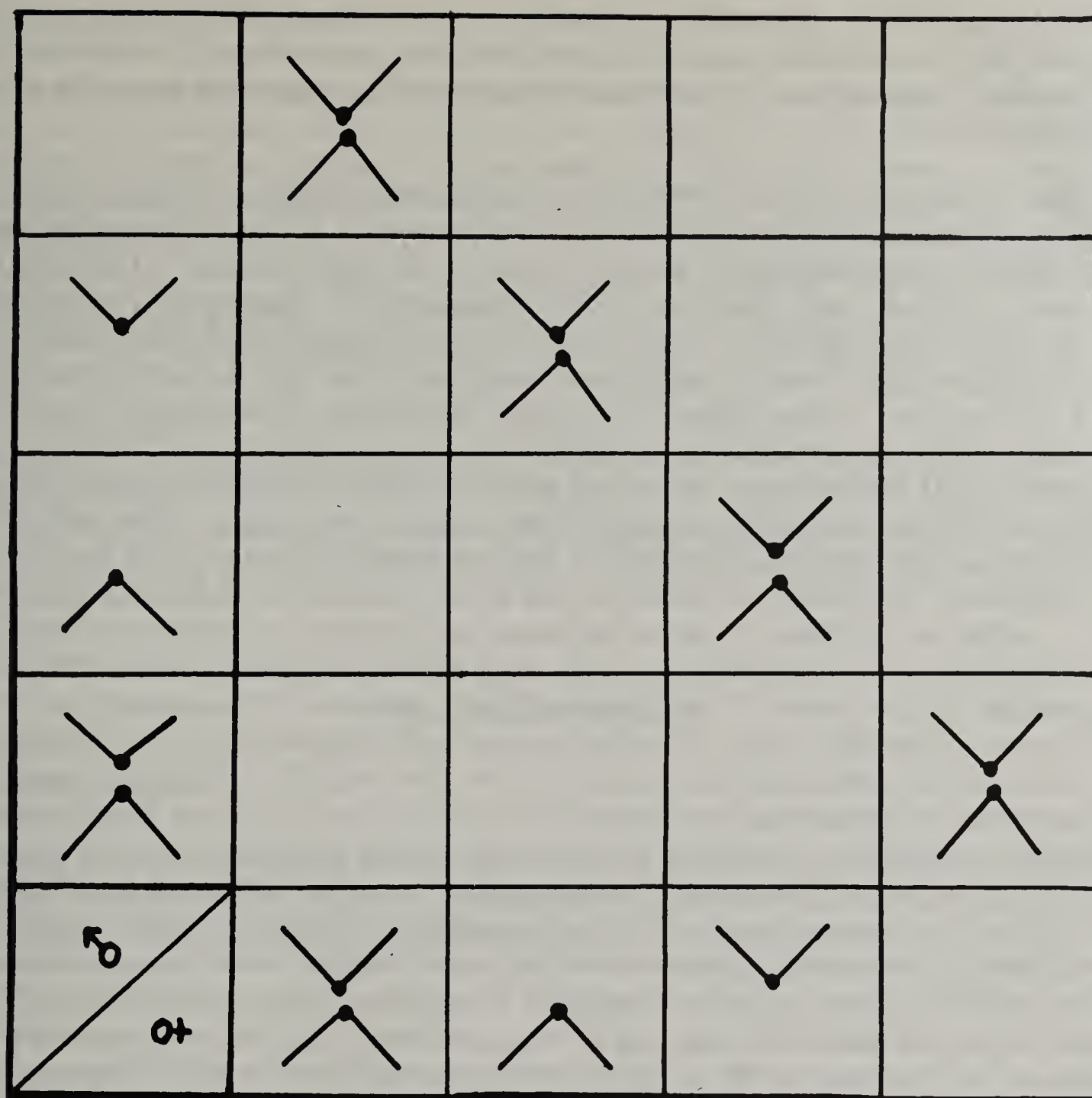


Fig. 2. —The meiotic behavior of a compound line. Only those surviving zygotes are shown. The viability of a compound line is 25% that of standards.

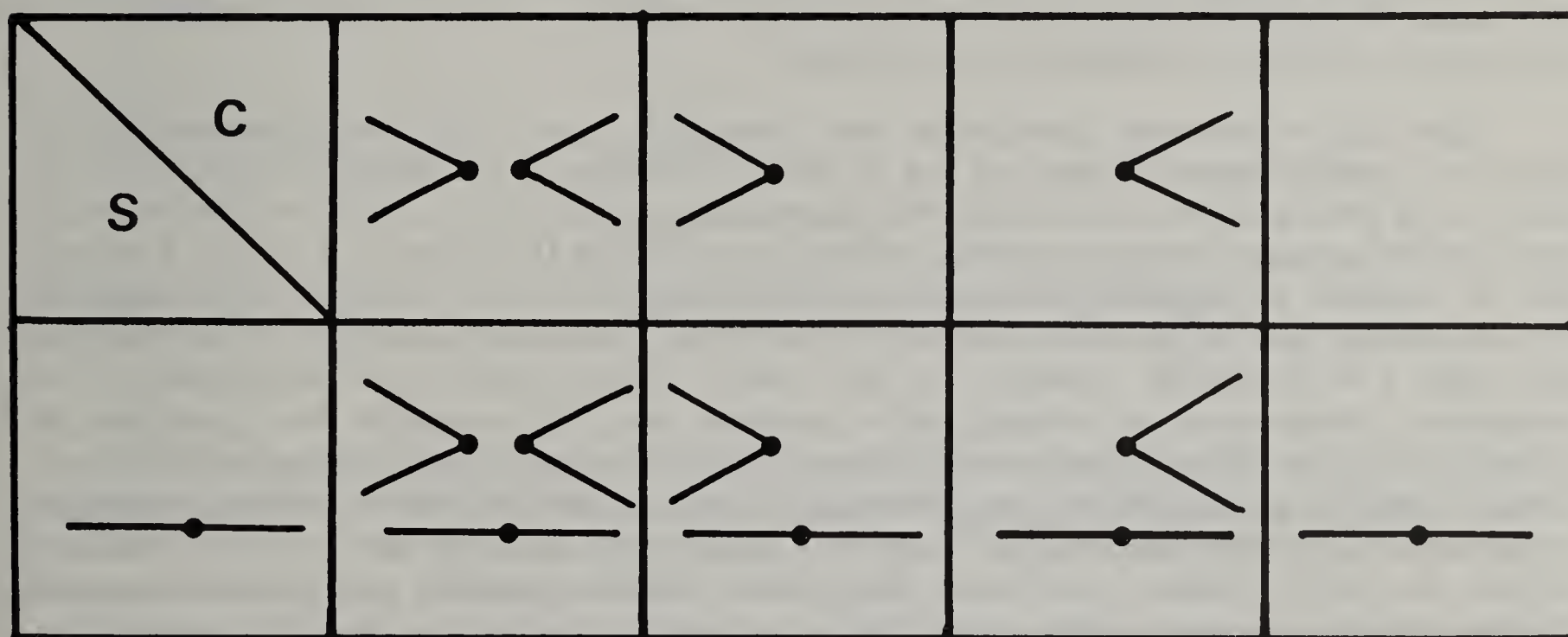


Fig. 3. —The result of crossing a compound strain (C) to a standard strain (S). All zygotes are aneuploid and die in the egg stage.

displace native standards under cage conditions even at the initial ratio of 30:1 (Cantelo and Childress 1975). It is clear that, for optimum success in control programs, insects should be collected from the wild and be genetically manipulated in the laboratory to synthesize compounds as rapidly as possible, prior to release in the field.

Field cage experiments have revealed that under two widely differing sets of natural environmental conditions, it is indeed possible to displace standards, and in the case of native-derived compounds competed against laboratory standards, even at the initial ratio of 5:1 (Fitz-Earle et al. 1975). Conversely, Cantelo and Childress (1975) simultaneously introduced laboratory-derived compounds and native standards in the ratio of 100:1 into field cages baited with tomatoes. After a few weeks they found that the compound strain had disappeared but the native standard strain survived. The explanation for the failure of this trial was based on the apparent failure of the compound strain to utilize the tomatoes as an oviposition site. In another study, 2500 adult pairs of a strain of compound 2 *D. melanogaster*, augmented with 500 newly hatched larvae, were released into a wine cellar in an attempt to test the principle of insect replacement using compounds (McKenzie 1976). The compound line used had a background that was partially of native origin but, by virtue of the mode of synthesis, the compound 2 left as well as the compound 2 right, was quite probably patroclinous in origin as a product of nonsegregation, and therefore of laboratory origin. In any event, the compound strain was eliminated from the cellar within 180 days. The principal factor cited as being responsible for the demise of the compounds was migration of inseminated native females from areas adjacent to the cellar, since the cellar was not sealed against migrants (McKenzie 1976). During the period of the experiment the extracellular native flies would be undergoing a natural rise in numbers characteristic of *Drosophila* populations in the fall. At no time was there an attempt to measure the degree of migration, especially into the cellar, as the external population increased and hence any potential success of the release technique against intracellular indigenous flies was obscured. The impact of migration upon released compounds engaged in competing against standards could have been measured by comparing cages (or even cellars) established in known compound to standard ratios and then subjecting them to various stratagems of migration and non-migration. An additional problem relates to the fact that at the beginning of the experiment the cellar temperature was at 13°C which corresponds to a generation time of approximately six weeks and an adult lifespan of 100-120 days in *D. melanogaster*. The decline of the compound insects in the cellar could therefore be attributed equally to unilateral aging and death at the 13°C temperature, as to competition by resident standards or, as suggested by the author (McKenzie 1976), as to displacement by native migrants. The cellar experiment was unable to distinguish between these possibilities.

The ideal field test is to generate a stock of unmarked compounds whose genetic composition was completely of native origin (i.e., all chromosomes) and to compete these insects against the same native strain. The difficulties of generating the compounds are prohibitive and of course the absence of a marker in either the compound or standard makes evaluation of the experiment possible only if test matings or chromosome squashes were conducted.

Open field replacement experiments with compounds have so far been unsuccessful for a variety of possible reasons though not due to intrinsic weakness in the technique. Fruit piles that were free of *Drosophila* were inoculated with large numbers of laboratory compound flies (as well as their developing stages) bearing ostensibly inconspicuous markers (Fitz-Earle et al. 1975). The hope was to establish a population of compounds that would resist any random native migrants. Notwithstanding that one pile was consumed by black bears, *Ursus americanus*, none of the remaining fruit piles was successfully colonized by the released insects. Such factors as dispersal of the compounds, displacement by migrant native standards and field mortality were postulated as contributors to the failures. Cantelo and Childress (1975) also released marked compounds into open fields of tomatoes at two different sites. Although the ratios actually achieved of released compounds to indigenous native standards were 62:1 and 91:1 respectively, the compound strain was unable to replace the native standard population. The failure of these particular experiments was again attributed to the reluctance of the released flies to oviposit on the tomatoes. Recently, releases have been made of large numbers of *L. cuprina* compounds in the larval stage over an area of 300 square kilometers with a view to assessing the ability of the strain to survive and mate in the wild, and compete with native insects (G.G. Foster, personal communication).

One of the major disadvantages of compound-autosome lines is that they have egg hatches of 25% or less in *D. melanogaster* and 10.6% in the one existing *L. cuprina* compound autosome line (Foster et al. 1976). With the likelihood of comparably low values being found in other insects, the search for a chromosome rearrangement that was completely genetically isolated from standards but has higher viabilities was clearly a priority. A new combination of chromosomal arrangements, that was first generated by Grell (1970), is the subject of the experimental data reported in this article. Grell (1970) constructed a strain of *D. melanogaster* whose homologous left arms of chromosome 2 were attached in the manner of a compound, but whose right homologous arms, called 'fragments', were detached (Fig. 1c). Such lines should for completeness be termed compound-fragment combinations but for brevity shall be designated hereafter as 'fragments'.

This paper presents experimental evidence consistent with observations on the meiotic behavior of fragment lines (Grell 1970), as well as a demonstration of their genetic isolation from standard strains. In addition cage replacement studies with fragment strains are described involving marked laboratory-derived strains in competition variously with unmarked laboratory and native standard flies.

Materials and Methods

Strains and Their Derivation

The lines of *D. melanogaster* used in the experiments are listed in Table 1. The compound autosomes are reversed metacentrics and in some cases are given code letters for location of synthesis (S-Storrs, Conn; V-Vancouver, B.C.) and synthesizer (H-Holm; T-Tabatabaie), together with a number.

Table 1.—The fragment and standard strains of *Drosophila melanogaster* used in the experiments.

Strain	Origin
C(2L), <i>dp</i> ; F(2R)1, <i>bw</i>	As described in Grell (1970); obtained from Oak Ridge, Tenn.
F(2L), <i>nub</i> ² <i>b pr</i> ; C(2R), <i>cn</i>	Obtained from Oak Ridge
C(2L)VH1, <i>lt</i> ; F(2R)VH2, <i>bw</i>	Derived in this laboratory in the style of Grell (1970)
C(2L)VT9, <i>Cy</i> ; F(2R)VH1, <i>Pin</i>	As above
C(2L)SH1, \pm ; F(2R)VH2, <i>bw</i>	As above
\pm/\pm	Oregon-R wildtype
\pm/\pm (OK-S)	Native Okanagan — Summerland wildtype

All of the mutants used as markers on the compound arms or fragments are described in detail by Lindsley and Grell (1968). The construction of the first fragment line (C(2L), *dp* ; F(2R)1, *bw*) is recorded in Grell (1970). Subsequently a number of other fragment lines was generated in this laboratory including those strains used in these investigations.

The standard strain used in the studies was Oregon-R and is designated here as \pm/\pm . The native strain employed in the experiments was derived from one of many *D. melanogaster* collected from a remote fruit dump on the outskirts of Summerland in the Okanagan Valley of British Columbia, Canada. It is given the designation here of \pm/\pm (OK-S).

Laboratory Tests

Hatch and viability studies of a fragment line were conducted according to the following procedure. Thirty C(2L)SH1, + ; F(2R)VH2, bw virgin females were aged for three days and placed individually in numbered shell vials containing standard cornmeal-agar medium with two males of the same strain. Every 24 hours these parents were transferred to fresh vials and the eggs were counted. The egg laying studies were continued for five consecutive one-day broods. For broods 2 and 3, the number of hatched eggs was determined 36 hours after the parents had been transferred. The results of this experiment are reported as Experiment 1a in Table 2. Following eclosion, progeny were counted in all five broods and the total number of eggs and progeny from these broods are recorded in Table 2 as Experiment 1b.

Table 2.—Hatch and viability studies of the fragment line C(2L)SH1±/± F(2R)VH2, bw.

Experiment Number	Eggs			Adults	
	Total laid*	Total hatched	Percent hatch ± SE	Total recovered	Percent recovery ± SE
1a	723	352	48.6 ± 1.8	263	36.4 ± 2.2
1b	1585	—	—	645	40.7 ± 2.1

* 30 females; 1a—two one-day broods; 1b—five one-day broods.

Matings were made between males of three different fragment lines and virgin females of the standard strain ±/± (Table 3). Fifty single pairs of each cross were set up in shell vials. The furthest developmental stage reached by the progeny of each pair was subsequently recorded.

Cages and Growth Conditions

The insect cages used in the investigations were Plexiglas® cubes of side 46 cm, equipped with air vents at the top covered with nylon screening and a nylon-sleeved opening at the front to permit access to the flies, food dishes and water vessels. Open food dishes containing approximately 50 ml of standard cornmeal-agar medium were introduced every three days until a total of seven dishes were in the cage at any one time. A covered water vessel was retained in each cage to ensure high humidity conditions. All experiments were conducted in a laboratory, the temperature of which was held at 24.0±1.0°C.

Design of Cage Experiments and Sampling Procedure

Unmated males and females both from the fragment and from the standard strains were aged for 3-4 days and then released into cages in the initial ratios given in Table 2. The fly populations in each cage increased in size over continuous generations. Approximately two weeks after releasing flies into a given cage, and subsequently twice a week until fixation, a random sample of approximately 1000 flies were lightly anesthetized with ether, classified according to phenotype, counted, and then returned to the cage. Fixation was defined as having been reached when two consecutive samplings revealed exclusively fragments or standards. The frequency of fragment flies in each sample was calculated and recorded. The number of days to fixation was subsequently deduced.

Results and Discussion

Laboratory Tests

The results of the egg hatch experiments, shown in Table 2, Experiment 1a, demonstrate that in the fragment line tested approximately 50 percent of the eggs hatched. This finding is consistent with

the predictions of the meiotic behavior of compound-fragment combinations (Grell 1970) in that it clearly implies that the fragments regularly segregate during meiosis but the compound 2L assorts at random, as depicted in Fig. 4.

The total recovery of adults for the same line was in the order of 40 percent (Table 2, Experiment 1b). While this indicates a measurable loss of progeny during the larval and pupal stages, it is clearly a marked improvement over compound strains from which only 25 percent or less of the eggs hatch. From these results it would appear that the theoretical equilibrium between fragment and standard strains is in the order of 2:1 and therefore that the fragment lines could provide a superior system to the conventional compound approach.

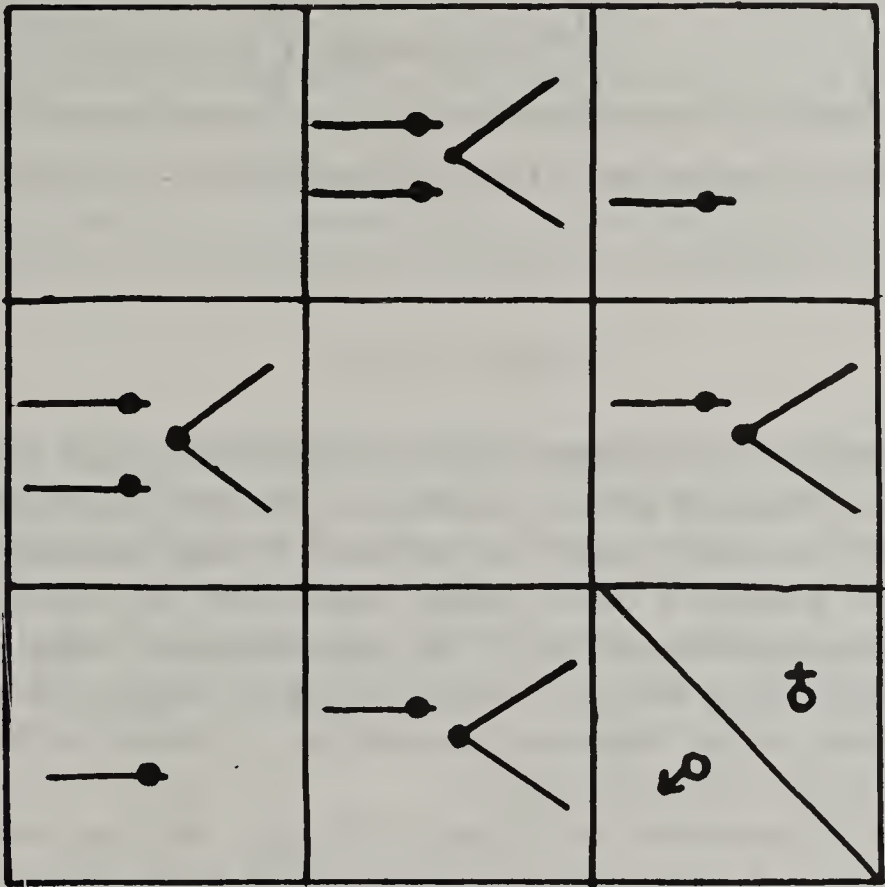


Fig. 4. —The meiotic behavior of a fragment line. Only those surviving zygotes are shown. The viability of a fragment line is 50% that of standards.

In the second set of experiments in which males of three different fragment lines were pair mated to standard females no progeny was recovered (Table 3). This data confirms the fact there was complete genetic isolation between fragment and standard strains as depicted in Fig. 5. In addition, it is interesting to note that some aneuploid combinations were viable up to and including the pupal stage (Table 3). It is suspected that these progeny are trisomy 2L, disomy 2R; that is, they carry one standard second chromosome, one fragment 2R and a compound 2L (Fig. 5). The importance of this observation is that it demonstrates the potential for competition for food by a class of hybrid progeny that will not contribute to the adult population.

Table 3.—Matings between fragments and standards.

Fragment Males	Standard Females	Pair matings*	Farthest stage reached*			
			Egg	Larva	Pupa	Adult
F(2L)2, <i>nub</i> ² <i>b pr</i> ; C(2R), <i>cn</i>	±/±	50	36	7	7	0
C(2L)VH1, <i>lt</i> ; F(2R)VH2, <i>bw</i>	±/±	50	22	5	23	0
C(2L)VT9, <i>Cy</i> ; F(2R)VH1, <i>Pin</i>	±/±	50	12	6	32	0

* Number of vials.

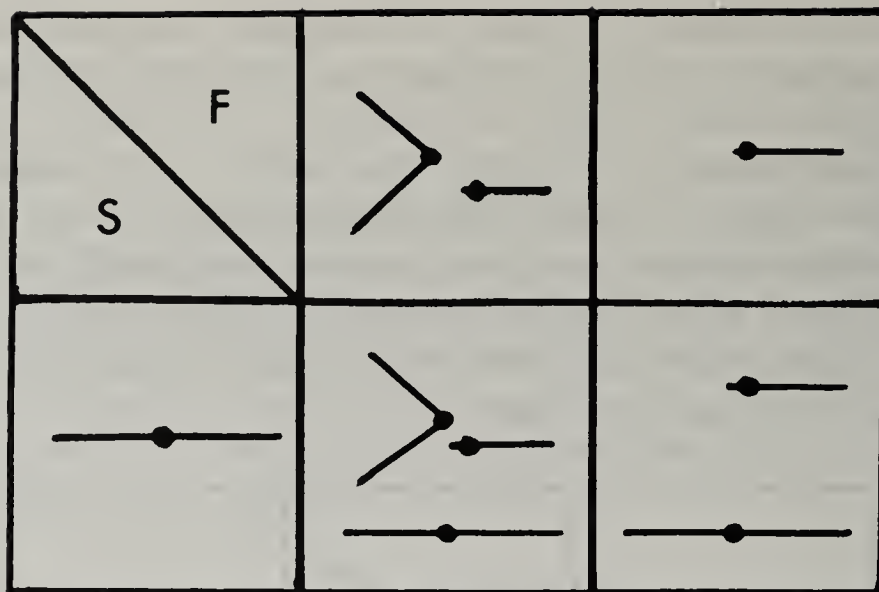


Fig. 5. —The result of crossing a fragment line (F) to a standard line (S). All zygotes are aneuploid and die by the pupal stage.

Cage Experiments

The cage experiments with fragment strains described in this report were not conducted coincidentally but in the sequence listed in Table 4. The earliest competitions were made using fragment strains available from stock centers or on hand in this laboratory. The failures of the first four lines to compete out standards at the ratios tested were not unexpected and were viewed as consequences of the genetic markers carried by the fragment lines, rather than as an inefficacy of the technique (e.g., *dp* — dumpy wing and *Cy* — curly wing, both impair the flight performance of flies). This prompted the synthesis of the fragment line carrying a marker that was considered to be far less innocuous, namely C(2L)SH1, + ; F(2R)VH2, *bw*.

When competed with laboratory wild-type (+/+) flies, this fragment line became fixed in the cages established at 5:1 and 4:1 ratios but was unsuccessful at the ratio of 3:1 (Table 4). The same fragment strain, when established with a native standard (+/+ (OK-S)) at 5:1, was likewise successful in displacing the standard though the time to fixation was considerably longer than the equivalent experiment using +/+ (Table 4). The speculation is that the native standard competitor may restrict

Table 4.—The results of competitions between fragment and standard strains at various release ratios.

Fragment strain	Standard strain	Ratio	Fixation*	Days to fixation
C(2L), <i>dp</i> ; F(2R)1, <i>bw</i>	±/±	25:1	F	80
F(2L)2, <i>nub</i> ² <i>b pr</i> ; C(2R), <i>cn</i>	±/±	50:1	F	67
C(2L)VH1, <i>lt</i> ; F(2R)VH2, <i>bw</i>	±/±	15:1	F	53
		15:1	F	97
		10:1	F	105
		5:1	F	71
C(2L)VT9, <i>Cy</i> ; F(2R)VH1, <i>Pin</i>	±/±	15:1	F	73
C(2L)SH1, + ; F(2R)VH2, <i>bw</i>	±/±	5:1	S	74
		4:1	S	133
		3:1	F	133+
C(2L)SH1, + ; F(2R)VH2, <i>bw</i>	±/± (OK-S)	5:1	S	94

* Of fragment ; F—failure ; S—success.

the success of the fragments at lower ratios. Experimental cages at the ratios of 4:1 and 3:1 are currently testing this conjecture and the findings will be reported upon completion.

A question that requires further elucidation concerns the consequences of the aneuploid hybrids between fragments and standards alluded to earlier, upon the overall effectiveness of the replacement. These hybrids as larvae place an added strain on the system by competing with the fragment and standard lines for food, which should cause a reduction in the total number of surviving adults. At this time, it is not possible to assess the impact of these hybrid larvae upon the effectiveness of the overall population replacement by fragment strains.

With a view to adding impetus to fragment lines, strains have recently been generated in which native material is incorporated into the fragment arms and background, but in which there are no markers. Results of experimental competitions between such marker-free native fragment lines and marked laboratory and native standards will be published elsewhere. It is anticipated that these new native fragment strains, which are extremely vigorous in culture, will prove to be the most effective in displacing the standards even for ratios at or close to the theoretical equilibrium for fragments of 2:1. If this is in fact the case, then the compound-fragment combination will have been demonstrated to be the most effective genetic tool for population replacement available to date.

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Current Status of Genetic Control of Hessian Fly Populations With the Dominant Great Plains Race^{1, 2}

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ABSTRACT

Laboratory, field cage, and small-scale field tests of the dominant avirulent Great Plains race Hessian fly, *Mayetiola destructor* (Say), in a program for genetic control of field populations in the eastern soft wheat region all clearly showed that populations of native flies can be suppressed. The Great Plains flies were fully competitive with the native flies, further evidence that this method of control is promising. A final decision concerning the practicality of the technique can be made after better rearing methods have been perfected and larger field experiments are conducted.

Increasing interest in genetic manipulation to control insect populations has produced a great number of papers that deal with the various aspects of genetic control. LaChance and Knipling (1962) presented calculations supporting the feasibility of using insects with inherited factors to control their own populations. Although Serebrovskii (1940) first postulated the theoretical reduction of native populations by genetic methods, it was the successful eradication of the screwworm, *Cochliomyia hominivorax* (Coquerel), from the southeastern United States (Anonymous 1962) that encouraged scientists to use insects to mediate their own destruction. Screwworm eradication was achieved by using the sterile male insect control method whereby large numbers of sterile males were released in the native population. Other methods that require high ratios of released to native insects have been proposed that usually involve one or more of the following: cytoplasmic incompatibility (Laven 1967), chromosomal translocation (Serebrovskii 1940, Curtis 1968, Wagoner 1969), inherited sterility (Proverbs and Newton 1962, North and Holt 1968), deleterious recessive genes (LaChance and Knipling 1962, McDonald 1970), segregating-distorting chromosomes (Hickey and Craig 1966, Sandler and Novitskii 1957, Wagoner 1968), or dominant conditional lethal genes (Masaki 1968, Hogan 1966, Klassen et al. 1970a, b).

A conditional lethal permits an insect to survive in one environment but not in another (Knipling 1960). To be useful for insect suppression, a conditional lethal trait must be expressed easily under certain circumstances. Klassen et al. (1970b) discuss the genetic differences that occur within a species with regard to ability to undergo diapause, response to diapause involving stimuli, duration of diapause, temperature limits of diapause termination, optimum temperature for diapause termination, ability to develop cold hardiness, thermal constants and temperature thresholds for development, choice of hibernial niches and behavioral traits associated with survival during inhospitable seasons and ability for diapause, its duration and response to conditions that involve to

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terminate it. As pointed out by Klassen et al. (1970b), such genetic differences must exist so that adaptations of insects to climate may be appropriate to their locality. Inappropriate adaptations are lethal under certain conditions, and so are conditional lethal traits. We may use a conditional lethal trait or a combination of conditional lethal traits to suppress or eradicate insect populations.

One example of a conditional lethal trait is the inability of the Hessian fly, *Mayetiola destructor* (Say), to live on resistant wheats. The Hessian fly, a destructive pest of winter wheat in the United States, is a small Diptera that according to its well-documented biology has 2 generations per year with emergence restricted to two, 1-month periods throughout most of the winter wheat growing region. Hessian flies are usually controlled by using resistant cultivars or by planting after the "fly-free" date. However, the widespread use of resistant cultivars has resulted in the selection of races (biotypes) having the ability to infest specific resistant cultivars. Six such races are now recognized as occurring in the field (the Great Plains race in central and western Kansas (Painter et al. 1931), Races A, B, C, and D (Gallun et al. 1961), and Race E (Hatchett 1969) in the eastern soft wheat region). They differ in ability to infest cultivars of wheat, *Triticum aestivum* L., that have specific genes for resistance. In studies of the nature of genetic differences between Hessian fly races, Hatchett and Gallun (1967) found that the inability of the Great Plains race to survive on resistant wheats was dominant to the ability to survive on susceptible wheats. Further, the expression of this trait is conditional. In the environment of a resistant plant, the larvae dies; however on a susceptible plant cultivar, the larvae survive.

The genetic interrelationships that exist between the Hessian fly races and resistance was discussed in several papers (Gallun and Hatchett 1969, Hatchett and Gallun 1970, Gallun and Hatchett 1968). The Great Plains race Hessian fly was suggested for use in an autocidal control program (Hatchett and Gallun 1967) and Gallun and Hatchett (1968) hypothesized that the introduction of the Great Plains race into areas where resistant soft wheats were being grown would result in elimination of all offspring from crosses of Great Plains by native Hessian flies as well as all progeny of crosses of Great Plains and Great Plains. Then flooding of the eastern races with the Great Plains race would serve as an effective method of control by selection against the recessive virulent races.

This hypothesis was tested in a step-by-step program initiated under defined conditions. The first test was conducted in the greenhouse with laboratory populations of Race B flooded with varying populations of Great Plains race. In these greenhouse tests, laboratory populations of Race B were controlled and eradicated in 2 generations by releases of 19:1 Great Plains race to Race B (Foster and Gallun 1972) (Fig. 1). However, these studies were made in the most ideal environment for both the wheat and the insect, and exact numbers of adults were used for each ratio. In the field, it would be impossible to release the short-lived fragile adults. Therefore, the next step was to conduct studies in field cages. This study was made by releasing the puparium (flaxseed) of the 2 races and allowing the flies to emerge to determine: (1) whether caged field populations of Race B Hessian flies could be controlled by overflooding with the Great Plains race introduced as flaxseed; and (2) what level of flooding would be required to control or suppress populations of Race B in field cages. We found that eradication occurred with 4 releases at a ratio of 9:1 or 2 releases at a ratio of 19:1 in field cages (Foster and Gallun 1973) (Fig. 2). Also, these data showed that synchronizing the released fly emergence with that of the native fly presented no real problems.

However, before we could test the program on a limited scale, the mating competitiveness, biology, dispersal, and methods of estimating populations of the Hessian fly had to be considered. Briefly, we found no serious adverse effects on mating competitiveness associated with the lethality. This, we concluded, was not the case because the dominant Great Plains race is a naturally occurring population on susceptible wheats in the hard wheat region of Kansas and mates readily with the eastern races of Hessian fly. Moreover, the resistant wheat cultivars are responsible for death of the offspring; thus, competitiveness was not affected by the factors causing lethality (Foster and Gallun 1972, 1973).

Then since the biology and dispersal are well-documented by McColloch (1923), we concentrated our next efforts on appraising a natural population, a must for any type of mass release program.

With most insect species, the number of insects per unit area varies greatly during various seasons. Therefore, we initiated a sampling program for the Hessian fly utilizing 3 fields over 4 generations of the fly so that levels of infestation could be determined over seasons (Foster and Taylor 1974). We determined that the distribution of larvae within a field is fixed by the female at

the time of oviposition, and that this distribution fits a negative binomial. Moreover, our data showed that a sampling plan for the Hessian fly produced estimates with an error of 10% or less of the mean so it could be used in estimating natural populations and in an evaluation of the autocidal control of the Hessian fly in a field test. This step in our program took nearly 3 years.

Currently, we are at the small field test stage of the study. We chose a field in southern Indiana that has a history of heavy infestations of the Hessian fly (Foster and Taylor 1974). The field was planted to the cultivar 'Arthur' though it had previously been planted to 'Monon'. (Since both Arthur and Monon have the same source of fly resistance (Gallun and Reitz 1971), the population was not disrupted by the introduction of a cultivar having a different source of resistance.) The field is ca. 8.5 acres and has been in continuous wheat for the 5 years we observed it and supposedly for 5 years before we began our observations, bringing the total to 10 years of continuous wheat.

A portion of the field was caged with sixteen 4x4x2-ft saran screen cages and used as a control area (protected from released flies). The remainder of the field served as the release area. Releases of the Great Plains race (as pupae) were made in September 1973 and 1974, and March 1974 and 1975 by spreading infested seedlings over the field. The flies were reared on wheat seedlings in the greenhouse so the number of puparia per seedling could be estimated and used to calculate the number released. From the estimated number of native flies in the field, the release ratio of 20:1 Great Plains to native fly was made. In September, the cages were left over the wheat until well past the time when complete emergence of flies had occurred, then they were removed and replaced in March before the 2nd release. When emergence was again complete (in ca. 4 weeks), the cages were again removed.

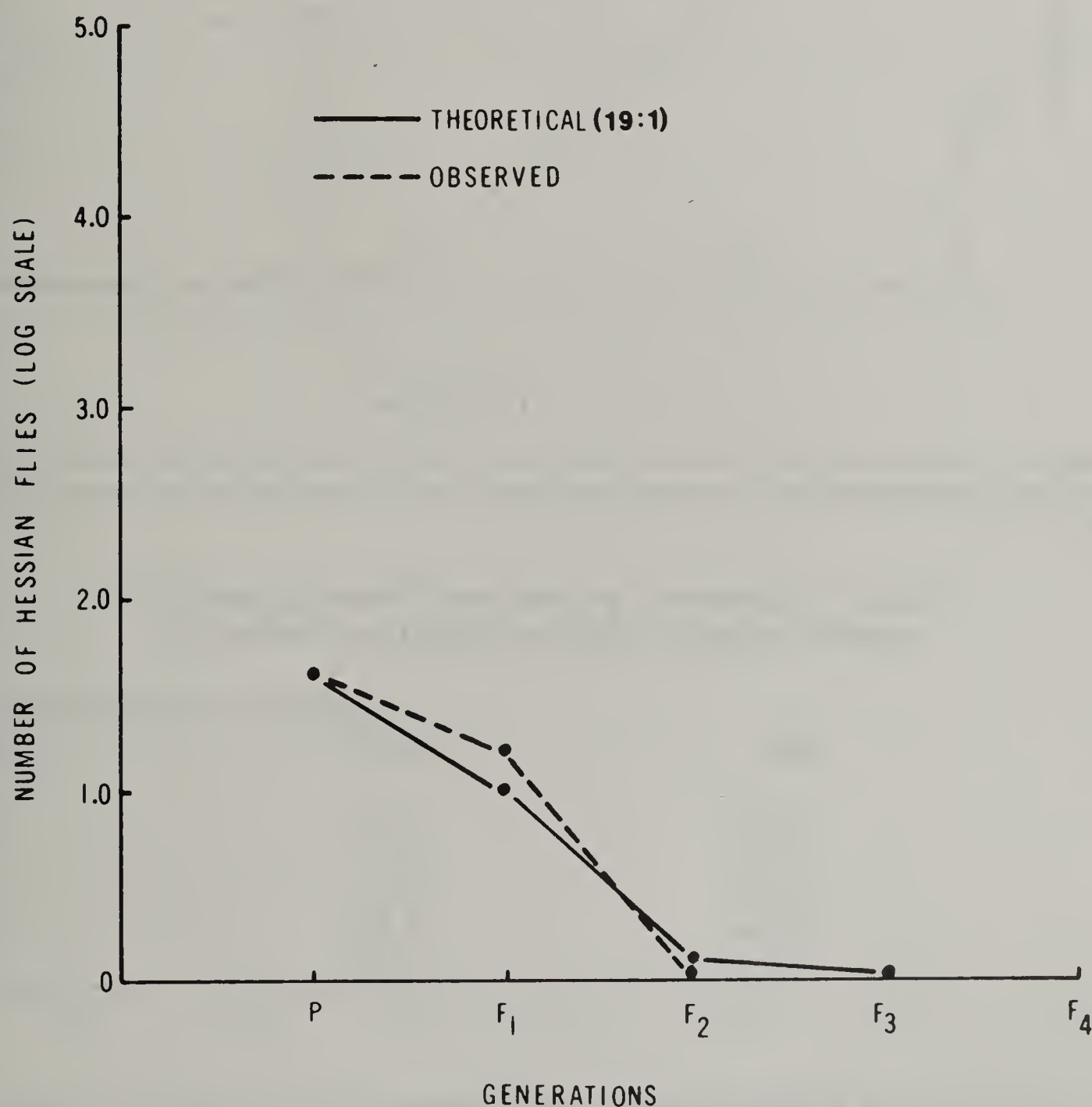


Fig. 1. —Trends of populations of Race B Hessian flies caged on Monon wheat starting with a base population of 40 Race B adults and continuing with a release each generation of 19:1 Great Plains race to Race B. (After Foster and Gallun 1972.)

After each generation, the fly population was sampled in both the release area and the protected control area. The method of sampling was systematic as had been described by Foster and Taylor (1974). From these data, we estimated the fly population in both the control and release areas (Table 1).

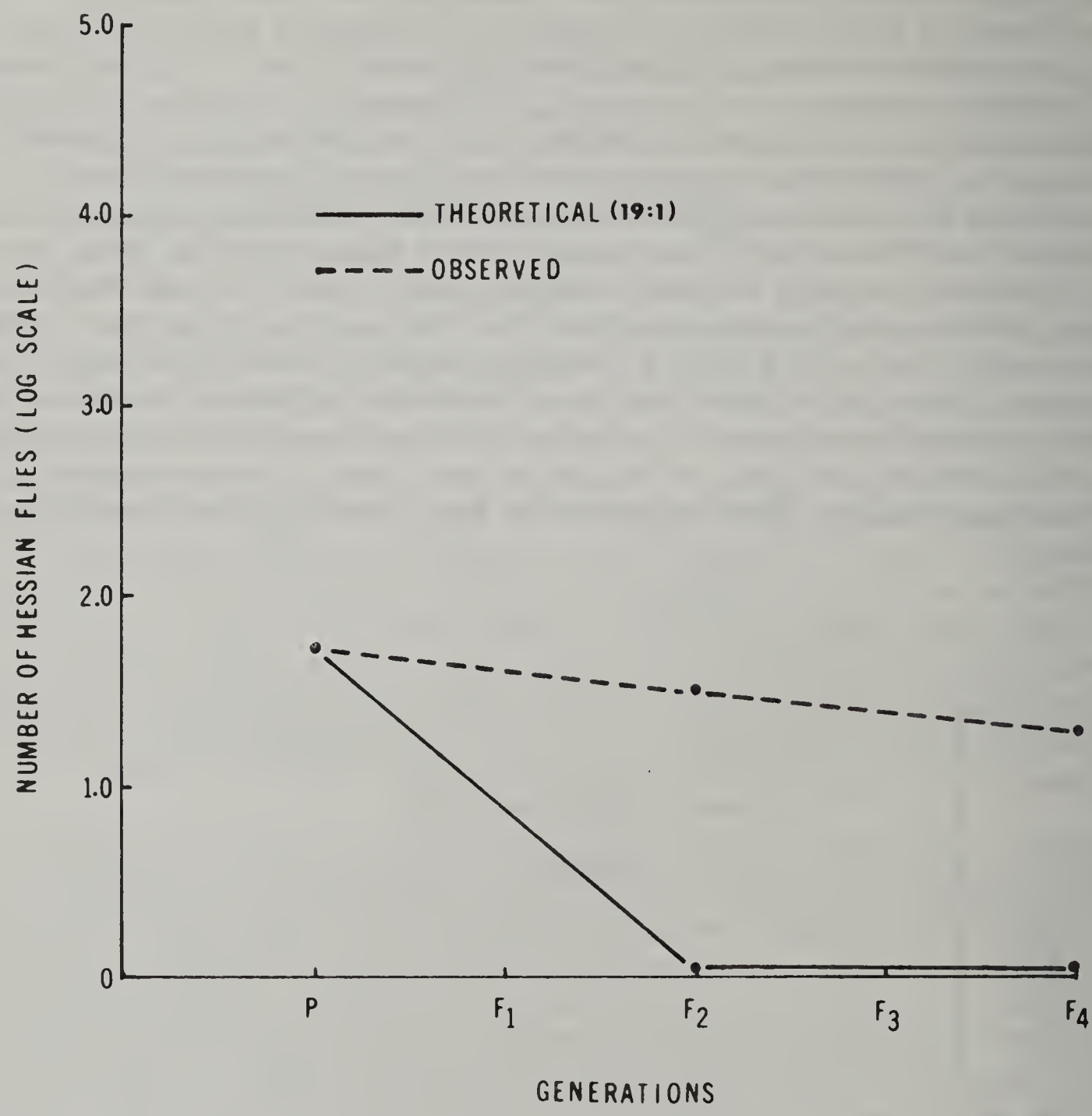


Fig. 2. –Trends of populations of Race B Hessian flies caged on Monon wheat starting with a base population of 50 Race B and continuing with a release each generation of 19:1 Great Plains race to Race B. (After Foster and Gallun 1973.)

Table 1.—Estimates of a population of Hessian fly made after successive releases of 20 Great Plains race:1 native race.

Estimate no.	Date	Number of flaxseed/50-culm sample	
		Control	Experimental
1	6/73	6.08	—
2	11/73	13.13	3.92
3	6/74	10.22	1.10
4	11/74	11.88	0.32
5	6/75	11.30	.05

The number of Great Plains race released in September 1973 was based on an estimate of the population made in the spring of 1973. Subsequent releases were made to maintain the desired ratio of 20:1 Great Plains race to native fly. The greatest impact on population suppression was made by the first 2 releases (Table 1). Meanwhile, the population in the field cages (protected from the release)

were minimum (Fig. 3). This result, we concluded, was a further indication that the Great Plains race is indeed competitive with the native flies. Also, we concluded that the Great Plains race definitely has potential to be used in a mass release program as a control for the Hessian fly.

The next step in the evaluation of a genetic control program for the Hessian fly must be a large-scale field study. A 40-50 acre field should be of sufficient scope to allow an economic evaluation. Also, such a study would provide a blueprint for an operational program. However, for such a test it will be necessary to mass rear the Hessian fly in greater quantities than our present capabilities allow. To date, this problem has not been resolved though we have been rearing 30 million flies/9-month period in the greenhouse (Foster, unpublished data). The present method

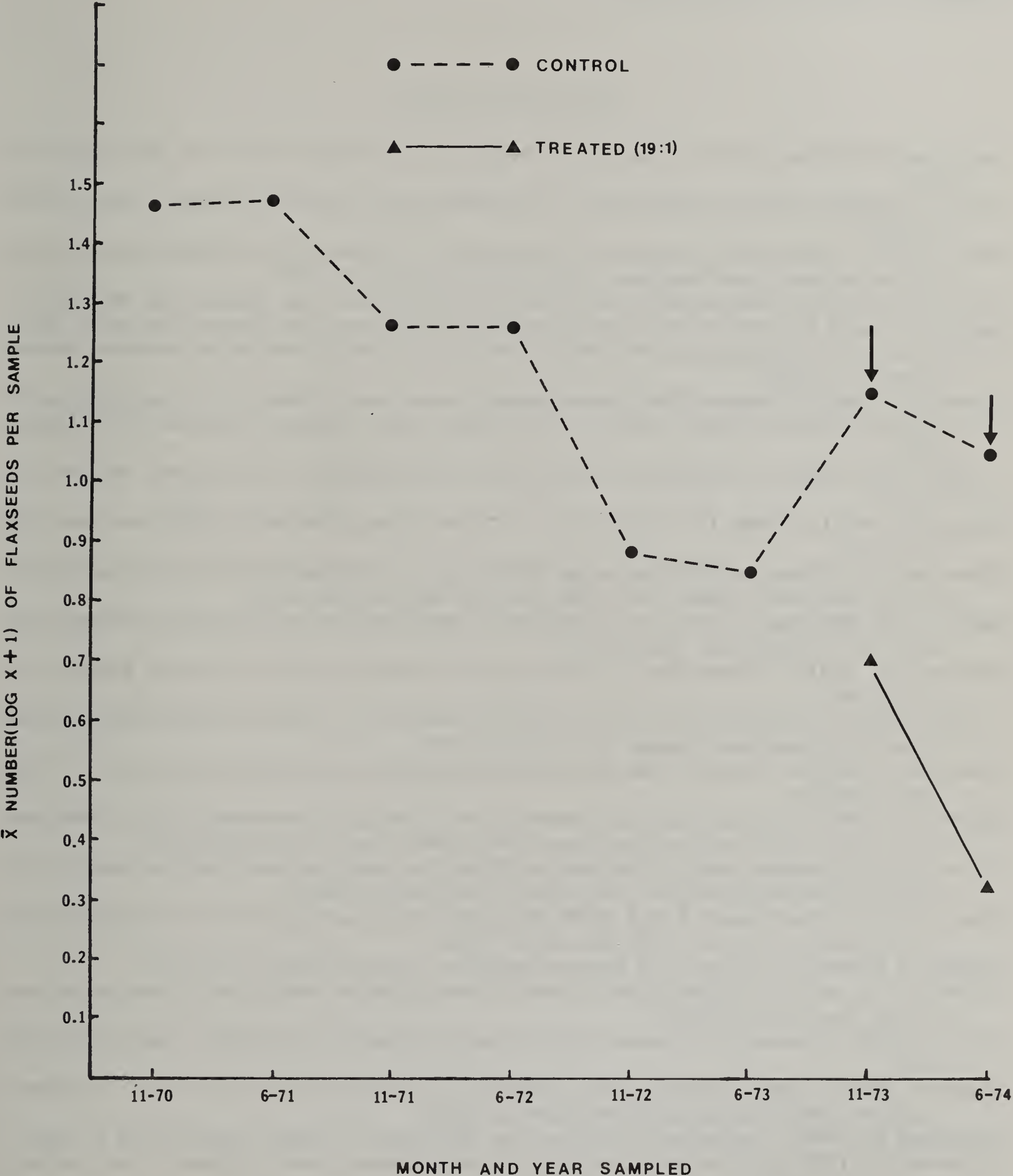


Fig. 3.—Trend of a field population of native Hessian flies on Monon wheat subjected to a constant release each generation of 20:1 Great Plains race to native flies. (Unpublished data.)

involves rearing the fly on seedling wheat with a turnover rate of ca. 30 days/generation at 21.1°C (Foster and Taylor 1975). Improved rearing methods and technology are the next step in implementation of the genetic control program.

In conclusion, we believe there are several reasons why the Hessian fly is a good candidate for an autocidal control program: (1) It usually has only 2 generations/year over much of the areas where winter wheat is grown, and the emergence period is restricted to a 2-3 week period each fall and spring. (2) Use of the Great Plains race eliminates the need for sterilizing equipment; also, both sexes transmit the avirulent gene and thus can be released. (3) The released flies are competitive with the native flies, an advantage over many sterile-insect release programs. (4) Finally, the released flies are not harmful to resistant cultivars of wheat because the agents that kill the insects are controlled by the genes for resistance in the host plant.

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Section 3: Physiology and Biochemistry

Insects in Extreme Environments

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Insects in the High Arctic¹

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ABSTRACT

The IBP study of arctic Truelove Lowland, 76°N 85°W, Devon Island, is discussed. One hundred and fifty-eight insect species in 8 orders, were collected over a 5 year period. At a meadow, 909 winged insects, at 54 mg oven dry weight, emerged $\text{m}^{-2}\text{yr}^{-1}$. Insect standing crop numbers and biomass are given for this meadow. Insects assimilate 0.8% of the yearly net primary production of the lowland.

Insect species diversity is reduced in the arctic (MacLean 1975). This stems from reduced plant diversity (Porsild 1964, Saville 1972) and the consequent reduction of habitat diversity, in arctic ecosystems. The evolution of diversity depends primarily on climatic stability and time (Dobzhansky 1950). The first arctic tundra probably appeared in the Queen Elizabeth Islands 6-8 million years ago; the first definitely determined tundra appeared about 1 million years ago (Hopkins 1974). Thus, tundra biota has had a comparatively brief time to evolve. The insect fauna is derived by reduction from lower latitude faunas, with limited *in situ* evolution at the species level (Downes 1964, 1965). This reduction pattern can be seen in latitudinal diversity gradients. A comparison of invertebrate species lists from IBP tundra sites, ranked according to species diversity, showed that diversity corresponded to site latitude (Ryan, in press a).

Western European arctic and temperate faunas are frequently well documented for limited areas (Nelson 1971, Luff et al. 1974, Journal, Zoology of Iceland). Most of the Western European arctic corresponds to the Canadian boreal forest sub-arctic (Rosswall and Heal, eds., 1975). The USSR contains most of the pale-arctic true tundra. Much of the Russian faunal information is unavailable in English, except for specific IBP (International Biological Program) exchange data (e.g., Chernov et al. 1975).

In this paper, I summarize information about insect diversity, and energy flow, on the coastal Truelove Lowland of Devon Island, 76°N 85°W. Specific details about this IBP project can be found in the summary of site research (Bliss, ed., in press). The invertebrate portion of this work represents 16½ man seasons spent at Truelove by 4 primary researchers, plus helpers, from 1970-74.

The site is an extreme environment. The lowland is 43 km², plus an adjoining 3.6 km² valley. It is surrounded on two sides by steep, 300-400 m cliffs behind which lies a 22,000 km² glacier. Jones Sound, which is ice-covered until about mid-August each year, forms the north and western border. The annual heat budget averaged 304 C day degrees above 0 (Bliss 1975). The active layer thaws to a maximum depth of 0.5 m, below which lies approximately 300 m of permafrost (Brown, in press). Much of the ground is frost patterned, and ice wedges occur at the ground surface of the most distinctive patterned ground.

¹ Paper No. 33, Devon Island Project, IBP.

1. Diversity

The lowland flora consists of 94 species of vascular plants (Bliss 1975), 175 bryophytes (Vitt and Pakarinen, in press), and 182 lichens (Richardson, in press). Eleven plant communities were recognized on the lowland, with 3 meadow types covering 71% of the land area. There are 7 lowland mammal species. Muskox, lemming, and weasel are permanent inhabitants, while polar bear, arctic fox, arctic hare, and arctic wolf are occasional visitors. Fifteen bird species (of 36 sighted, 1970-74) regularly breed on the lowland (Pattie, in press).

There are 241 known invertebrate species on the Truelove Lowland. Protozoa, (14) and especially Nematoda, (2) are treated superficially in the list. There are 199 arthropods with acknowledged probable gaps in the Acarina and Diptera Chironomidae. There are 158 insect species, belonging to 8 orders (determined by 25 specialists). Four orders are energetically insignificant. There is one known homopteran, a rare scale. There are 3 Coleoptera. The carabid *Amara alpina* occurs primarily near the Truelove River outlet. The staphylinid *Gynpeta* sp. is minute and rare, as is the dytiscid *Hydroporus polaris*. The trichopteran *Apatania zonella* is a lake dweller. I found 5 species of Phthiraptera. Since they are small, and their hosts rare, they are energetically insignificant.

The 4 significant orders are Collembola, Lepidoptera, Diptera, and Hymenoptera. Thirty species of Collembola are known from the Lowland; but the number may actually be less, due to disagreement between the 2 authorities making determinations. Fifteen Lepidoptera were collected. Two are butterflies, *Boloria chariclea* and *B. polaris*. *Olethreutes inquietana* and *O. mengelana* were the commonest moths. There were 64 species of Diptera collected, including only 21 chironomids — there are probably more. Species in the other families have been adequately collected and determined. The 39 Hymenoptera included 10 species of Symphyta and 29 of Apocrita. The 9 *Amauronematus* species (Symphyta) collected may not all be valid taxa, since this genus requires revision. All Apocrita are parasites, except for *Bombus polaris*.

Most but not all insect species inhabiting the Truelove Lowland were collected in this study. No orthopteroids, odonates, or neuropteroids occur at the site.

Lake Hazen, at 82°N on Ellesmere Island, has been thoroughly investigated entomologically (Oliver 1963, Downes 1964). Despite its more northerly latitude, it is warmer [397 C day degrees (Corbet and Danks 1974) vs. 304] and supports a more diverse flora [115 species of vascular plants (Saville 1972) vs. 94] than Truelove. Comparing taxa most likely to be collected, on a species-at-Hazen/Truelove-basis, shows Araneida (Leech 1966) to be 13/10, Coleoptera 3/3, Lepidoptera 17/15, Diptera (Culicidae, Empididae, Dolichopodidae, Syrphidae, Calliphoridae, Tachinidae) 16/11, and Hymenoptera Apocrita (except *Atractodes* spp.) 35/26. Thus, the Truelove fauna is as diverse, or slightly more so, than would be predicted by comparison with the Hazen site. Pt. Barrow Alaska is quite similar to Truelove in plant diversity (94 vascular plants and accumulated temperature (321 C degree days) (MacLean, pers. comm.). Barrow supports 345 known arthropod

Table 1.—Pterygote insect emergence production at the intensive study meadow site, 1972.

	Total winged Insects	Diptera			Hymenoptera	
		Lepidoptera	Nematocera	Muscoidea	Symphyta	Ichneumonidea
no. m ⁻²	909	0	893	13	0.8	1.8
mg* m ⁻²	54	0	34.3	18.6	0.7	0.6

*Oven dry weight.

Table 2.—Insect standing crops at the intensive study meadow site, 1972.

	No. m ⁻²	mg* m ⁻²	energy flow cal m ⁻²
Collembola	8737	42.6	250
Lepidoptera	0	0	0
Diptera	7116	97.8	
	(10600)	(146.7)	2618
Hymenoptera	2	1.5	58.6

*Oven dry weight

Table 3.—Summary of energy flow on the Truelove Lowland.

	Kcal m ⁻² yr ⁻¹
Net Primary Production	656
Consumer Assimilation:	
Muskoxen	6.9
Lemming	0.52
Vertebrate carnivores	0.08
Birds	0.005
All Invertebrates	30.9
Insects	5.2

species, almost double the Truelove fauna (Bohnsack 1968). Barrow is continental, and has been influenced by the Bering land bridge faunal exchanges (Ryan, in press a). Truelove Lowland is islandic, is isolated from southern continental influences by 500 Km of glacier, high plateau, and ocean, and is not near any major faunal interchange. Thus, Truelove should be less diverse than Barrow.

2. Energy Flow

The purpose of this IBP study was to measure energy flow m⁻²yr⁻¹. This is energy actually used, and is equal to all energy respired, and tissue produced, by the insects. Production can be defined several ways (Petruscewicz and Macfadyen 1970). The definition most useful for a broad ecological study is the amount of tissue which becomes available to the next trophic level (Odum 1971). Both parts of energy flow are not discretely measurable. The respiration of an individual can be measured; respiration of a population, in the field, cannot. The weight of a live individual can be measured; the weight, at death, of individuals in a field population cannot.

So I measured energy flow with the aid of a model (Ryan, in press b). The operation of the model is conceptually simple. An insect, between hatching from an egg and becoming a prepupa, gains a measurable amount of weight. Its respiration rate was measured over a range of temperatures and weights (Procter, in press). From these, the respiration rate was computed at every weight interval for the developing larva. The time required to grow to maturity was determined by calculating how much respiration must occur to produce the observed weight gain, given the constant "c". This "c" is an empirical constant, the ratio of Respiration/Growth. Some larvae die during development. These were estimated by assuming exponential mortality among developing larvae. Pupal and adult energy flows were calculated separately.

Specific information was required to operate the model. Adult insect emergence is one measure of production used for the model. Emergence was measured with 1 m² nylon screen emergence traps. Five traps were placed in selected locations, and collected insects were removed every 5 days. The

results of the intensive meadow site traps are shown in Table 1, in numbers and biomass emerged m^{-2} for the full season.

Standing crop information was obtained from weekly soil extractions made with Tullgren, Macfadyen, and O'Connor funnels. Soil cores were extracted to 5 cm. These were compared with extractions to 15 cm, and with extractions of animals added to sterilized cores, to estimate the actual populations. These results are shown in Table 2 as standing crop numbers and biomass. The estimated actual standing crops are given in brackets below the extracted quantities. Energy flow, calculated from this and Table 1 data, and information not shown here (Ryan, thesis in prep.), is shown in the final column.

How do the insects compare to the rest of the ecosystem? I have summarized information in the Devon Island book (Bliss, ed., in press) in Table 3. This is given as m^{-2} of the lowland, rather than of specific habitats, such as the meadow site discussed above. The table shows that invertebrates assimilate 5% of the net primary production, with insects getting 0.8%. Most invertebrate energy comes through the decomposition food chain, in the soil. Thus, these animals act like ruminants, but with their ruminant symbionts outside their bodies (analogy by Goksoyr, pers. comm.). In this cold-dominated ecosystem, where they are frozen nearly 10 months per year, insect energy flow is slightly less than the combined mammalian energy flow.

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Distribution and Isolating Factors in the Races of *Papilio machaon* (Lepidoptera: Papilionidae) in Central Himalaya

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ABSTRACT

Central Himalaya (Nepal) is inhabited by four races of *Papilio machaon*: *sikkimensis* east of Mt. Everest, at high altitudes; *rinpoche* west of it at high altitude; further west in the Daulaghi area there is the West Himalayan *ladakensis*; and in the lower areas there is *emihippocrates*. Breeding experiments have shown that there are genetic differences between *rinpoche* and *emihippocrates*. The isolating factors are meteorologic ones, precipitation and reduction of daylight by clouds. At below 40.000 lux *machaon* is inactive. The races living above and below the continuous cloud belt are unable to meet and genetic exchange, therefore, is impossible.

In Central Himalaya (Nepal) around Mt. Everest there meet two main groups of *Papilio machaon*, one coming from the east and the other from the west. This partition into two groups is due to the glacial age. The groups do not really meet, as there is a narrow isolating zone which prevents gene exchange. The isolating factor here is precipitation. The race *sikkimensis* coming from the east, is highly adapted to dry conditions, while the races *rinpoche* and *emihippocrates* to the wet monsoon conditions. Therefore, *sikkimensis* can be found only north and east of Mt. Everest, while *rinpoche* is known only from the southern slopes, and is fully influenced by the monsoon.

The western races *rinpoche* and *emihippocrates* live in the same area but at different altitudes. They are separated by a zone where none of them occur. This zone is the mean altitude of condensation and during the warm season there is a continuous cloud belt which reduces the daylight and measurements have shown that there are normal conditions at 25-30.000 lux. This light condition permits butterflies of Oriental origin, adapted to this altitude, still to be active.

One can, for example, see the impressive *Troides aeacus* flying in fog and rain. But *Papilio machaon* is not active below 40,000 lux. It is, therefore, not able to penetrate the cloud belt, which is a very effective isolating factor. The result of this isolation is a genetic difference between the two races. It was proved by breeding experiments which were done under exactly the same conditions for both races. Several characters remained stable under different environmental conditions. During spring and fall there are of course less humid conditions and the cloud belt disappears, but then only the lowland race is flying, the higher altitudes are too cold, and any intermingling is impossible. There is only one brood in the high altitude race, while in the lowlands there are 5 to 6 broods a year.

The special adaptation to high altitude conditions is a diapause. Breeding experiments indicate that the origin of this diapause is temperature and not photoperiod. Bred at 6°C minimum and 17°C maximum at 4000 m altitude produced brown diapausing pupae, those bred at 25°C minimum and more than 30°C maximum produced green pupae which hatched within 8 days. The reactivation of diapausing pupae came after a cold winter season with temperatures below zero followed by 20°C. Therefore, also for the multiple breeding lowland race, a short period of inactivity from November to February is evident in the Kathmandu area, where during this time the minima are from 5°C to zero. It is not yet proven whether this inactivity is a true diapause or just a quiescence. It is also of importance that the lowland race is not distributed below 1000 m altitude while the upper limit at the cloud belt is somewhere around 2000 m.

The third western race, *ladakensis*, which is distributed in the Western Himalayas, could (in Nepal) only be found north of Daulaghiri at high altitudes. It seems likely that this race, as opposed to *rinpoche*, is highly adapted to dry areas, as they are north of the main mountain range and in the Western Himalayas. *Ladakensis* and *rinpoche* meet at the northern Kali Gandaki valley but it is unknown whether there is interbreeding or not.

Compared with observations on the distribution of other butterflies it seems likely that species of palearctic origin which have immigrated into the Himalayan mountains and which are not adapted to the high humidity have a distribution limit at below 1000 mm annual precipitation and at light conditions below 40.000 lux. From this it can be understood why the southern slopes of the eastern Himalayas are so poor in butterflies. South of Mt. Everest for example there are only 6 non-migrating butterflies, while north of it, not more than 30-40 km away, there are more than 35 species. This gives a good impression of the zoogeographic conditions of this area and the limits of the Palearctic and Oriental areas.

Strategies of Low Temperature Adaptation

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ABSTRACT

Over the past two decades, controversy over the mechanisms responsible for low temperature tolerance, and specifically frost hardening, has arisen. The cryoprotective role of natural "antifreeze" compounds (i.e., glycerol, sorbitol, erythritol, etc.) has been reported by a number of researchers while others have questioned their apparent role(s).

This report will elaborate on the physiological and biochemical mechanisms that allow three species of overwintering insects to survive: 1. *Pterostichus brevicornis* an adult, Arctic carabid capable of synthesizing with varying thermal stress multi-molar concentrations of a single phase cryoprotectant (glycerol); 2. *Eurosta solidagensis* — a gall fly that demonstrates an ontogenetic pattern of survival common to many temperate species yet accumulates three cryoprotectants in sequence and, 3. *Coleomegilla maculata* — a ladybird beetle capable of modifying effective ice nucleator content while maintaining a fixed water content and independent of "antifreeze" substances.

Behavioral, ecological and physiological interrelationships enable overwintering stages to maintain activities normally restricted to "above-freezing" situations at temperatures as low as -60°C .

The mechanisms allowing for winter survival of northern insects faced with seasonal freezing encounters has been studied by relatively few investigators (Asahina 1966, Baust and Miller, 1970, 1972, Baust and Morrissey 1975, Morrissey and Baust 1976, Salt 1957, 1959, 1961, Somme 1964, 1965). Salt (1956) provided the first clues to the relationship between frost hardiness, glycerol and water content. Water content variations afforded little or no protection unless severe desiccation was experienced. In a later study (Salt 1959) it was shown that glycerol played a direct role in cold hardening the larvae of *Bracon cephi* by depressing the hemolymph freezing point (Fp) as much as 17.5°C and lowered the supercooling point (SCp) to -47°C . Somme (1964) and Asahina (1966) found that cold hardening was facilitated by increased glycerol levels in certain species.

However, the question of cryoprotectant involvement in frost resistance appears unresolved. Somme (1965) and Asahina (1966) have not conclusively correlated freezing tolerance with a cryoprotective compound in each species studied and have questioned whether in fact cryoprotectants play a significant role as suggested by Salt (1961).

One problem faced with the evaluation of the physiological basis of low temperature adaptation is not so much concerned with the experimental aspects of the problems, but with the teleologic interpretations assigned to experimental observations. The taxonomic scheme under which the Insecta are placed is mistakenly viewed as a homogeneous ordering of species. Taxonomic arrangements are nearly exclusively based on morphology and rarely relate to ecological or

physiological characteristics. Insects represent the most diverse group of multicellular animals and demonstrate unparalleled classes of adaptative variations. Yet, single species are generally less flexible in the face of acute environmental stress unless a "pre-adaptative" capacity (Prosser 1973) can be defined. The presence of adequate levels of cryoprotectants is essential to freezing tolerance although a single report (Somme 1964) provides apparent exceptions. That is, neither glycerol or sorbitol were identified.

The presence of a cryoprotective compound alone does not constitute *prima facie* evidence for freezing tolerance. Polyhydric alcohols act in two ways to afford protection (Fig. 1) (Baust 1973). The first is an "ice avoidance" mechanism based on physico-chemical considerations (Fp depression, increased fluid viscosity and inhibition of nucleators leading to extended SCp). The second is a protective role that follows supercooling. It may be viewed as a "hydration" effect in that the shifts of intra- and extra-cellular water pools are diminished as compared to freezing without a cryoprotectant. Cellular dehydration is reduced due to the extreme hydrophilic nature of glycerol. This results in a decrease in total ice content, maintenance of an intracellular liquid pool while the extracellular pool is solidified, reduced cell shrinkage, stabilization of the lipid moiety of membranes with the retention of membrane fluidity and inhibition of protein denaturation.

The first protective mechanism is afforded to any *in vitro* or *in vivo* systems naturally containing or supplemented with appropriate cryoprotective concentrations. The second protective mechanism, however, can only be realized by tissue systems capable of integrating their cellular chemistry while exposed to high cryoprotectant concentrations. High concentrations of glycerol are relatively toxic at above freezing temperatures. This toxicity is in all probability related to the lipid solvent action of glycerol which may result in lethal damage to membranes. Below freezing, invertebrate and vertebrate (Meryman 1970) tissues become less susceptible to cryoprotectant toxicity. The lower the sub-freezing exposure, the greater the tolerance to increased levels of polyhydric alcohols and the greater the concentration required for protection. In order for an insect to maximize the probability of surviving prolonged freezing, it should develop a capacity to modulate cryoprotectant levels while frozen and with fluctuating temperatures.

The presence of a polyhydric alcohol or related carbohydrate in high concentrations is in itself an inadequate criterion for evaluating the mechanism of low temperature tolerance evolved by any one species. It is essential to correlate with seasonal or induced variations in cryoprotectant concentrations such information as Fp depression, SCp fluctuation, lower lethal limits, behavioral relationships and/or physiological and biochemical relationships including the kinetics of enzyme systems, precursor levels and the functional limits of organ systems.

A second problem related to our understanding low temperature adaptation is the reverse process or warm acclimation. Upon thawing, many insects initiate reacclimation to warm temperatures immediately. In *Pterostichus brevicornis* this process is "irreversibly" completed within hours (Baust and Miller 1972) (Figs. 2, Table 1). Glycerol levels drop precipitously within hours after thawing and exposure to room temperature. When a threshold level of approximately 10 gm% is reached, the warm acclimation process proceeds independent of further chilling. At approximately this point, *P. brevicornis* becomes freezing intolerant. The rapidity of the warm acclimation process is overlooked in many laboratories and may lead to erroneous results.

Methods and Materials

Three species of insects will be reviewed respective of their strategies of low temperature adaptation: *Pterostichus brevicornis* — an adult, freezing tolerant Arctic carabid; *Eurosta solidaginis* — a gall fly demonstrating freezing tolerance in a portion of one developmental stage; and *Coleomegilla maculata* — a ladybird beetle that is freezing intolerant yet capable of modifying ice nucleator activity without a discernible cryoprotectant (polyhydric alcohol or low molecular weight carbohydrate).

Acclimatization and acclimation schedules along with assay techniques have been published for each species (Baust and Miller 1970, 1972, Baust 1972, Baust and Morrissey 1975, Morrissey and Baust 1976).

Results

Following a summer cycle and upon exposure to 0°C, *P. brevicornis* initiates glycerol synthesis (Fig. 3) (Baust and Miller 1970) which is accompanied by decreased Fp and SCp. Glycerol levels may

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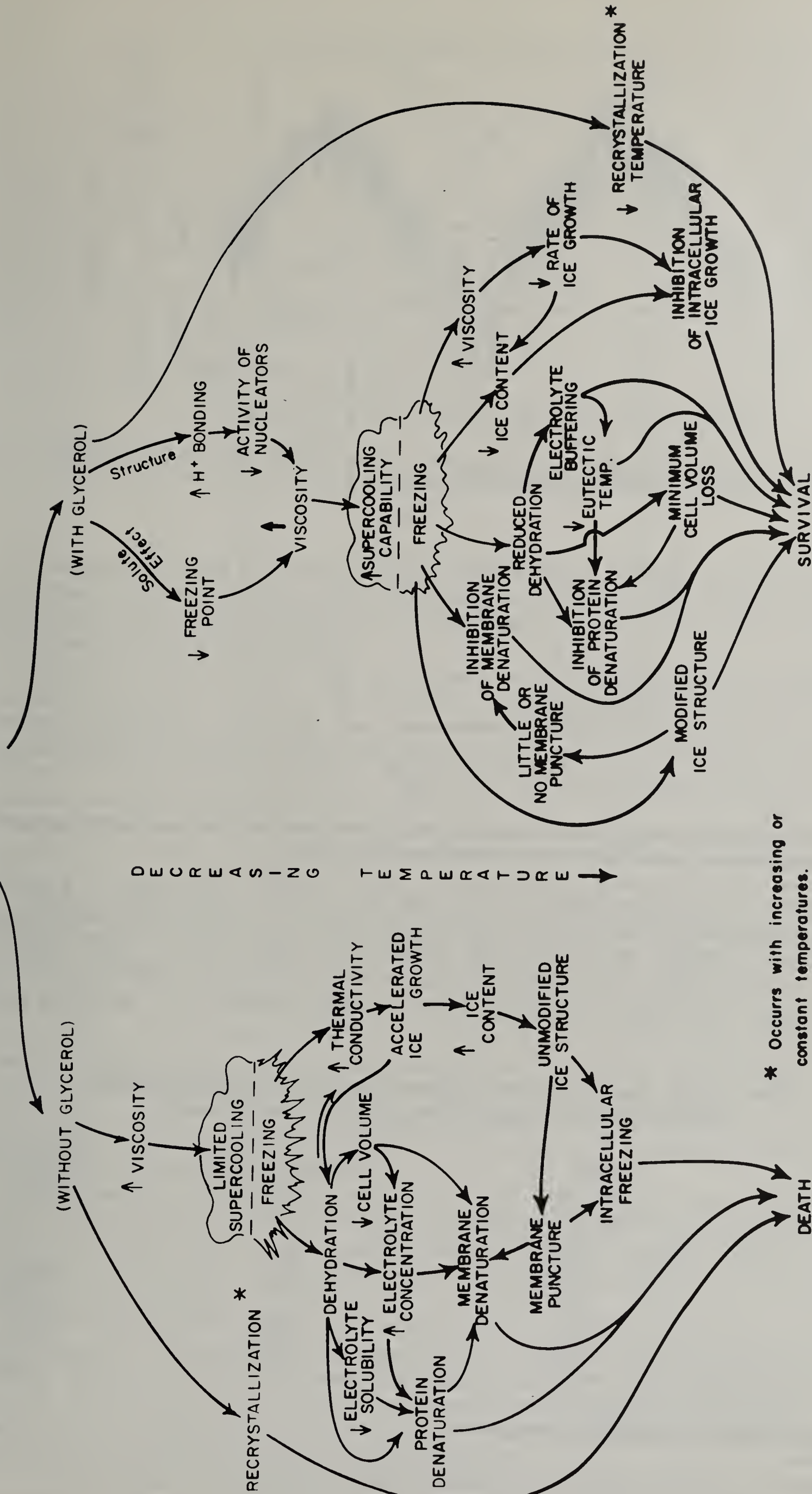


Fig. 1. — Schematic representation of the mechanisms of action of freezing damage and cryoprotection of glycerol in animal tissue (Baust, 1973).

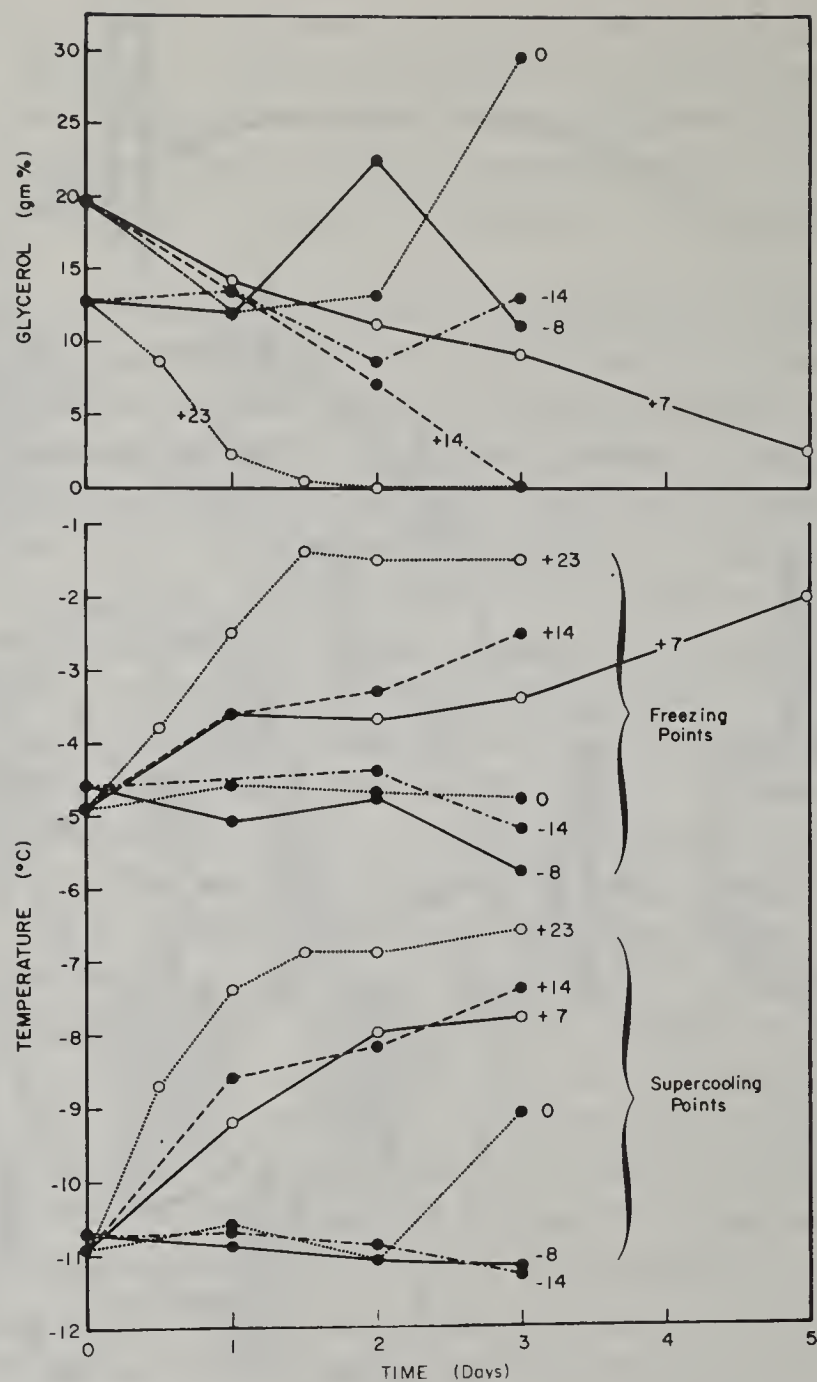


Fig. 2. — Variations in hemolymph glycerol content and freezing points and whole body supercooling points during warm (spring) acclimation in *P. brevicornis* (Baust and Miller 1972).

exceed 30 gm% while Fp's are depressed 4.5° and SCp's lowered 6.0°C (Fig. 4). Laboratory acclimation experiments yield similar results although the temperature extremes and time were not as extensive as those naturally encountered (Fig. 5) (Baust and Miller 1972). At each acclimation temperature between 0° and -10°C, an overshoot in glycerol concentrations is evident. This overshoot may be considered protective: an *anticipatory response* that functions in the event of a sudden temperature drop.

Table 1.—Rate changes per hour¹ of glycerol content, super-cooling points and freezing points during warm acclimation temperatures.

Temperature (°C)	Glycerol Conc. (gm%/hr.)	Supercooling Pts. (°C/hr.)	Freezing Pts. (°C/hr.)
-14	SI ²	0	—
- 8	SD ³	SI	SI
0	0.3	0.01	0.01
+ 7	0.3	0.07	0.05
+14	0.3	0.09	0.04
+23	0.7	0.09	0.09

¹ Represents rate changes over the initial 24 hour period.

² Slight increase.

³ Slight decrease.

(Baust and Miller 1972)

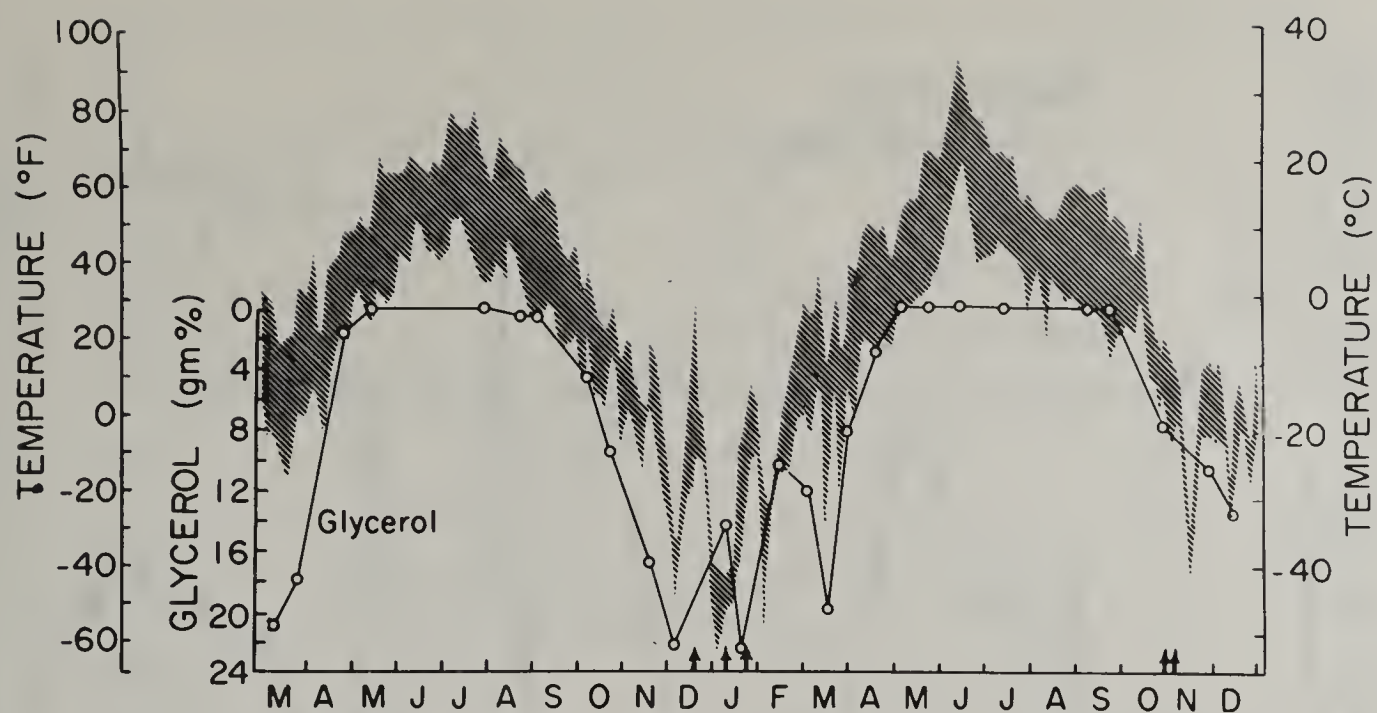


Fig. 3. — Seasonal variations in high-low ambient temperatures vs. means hemolymph glycerol concentrations. Latter scale is inverted. Arrows indicate major snow accumulations. (Baust and Miller 1972).

Preliminary attempts to correlate changes in glycerol with changing carbohydrate levels were not conclusive. Hemolymph trehalose levels *increased* as glycerol increased. Preliminary evidence in this and other species (Morrissey and Baust 1976) indicates that non-carbohydrate sources may play an important role in glycerol production.

The dramatic nature of the freezing tolerance strategy employed by this species tends to overshadow the pre-freezing adaptative advantages. Concomitant with biochemical changes are behavioral modifications. Following low temperature exposures (first frost) and the initiation of glycerol synthesis, *P. brevicornis* actively selects and maintains itself at subfreezing temperatures (Fig. 6) (Baust and Miller 1970). Specimens placed in a temperature gradient consistently aggregate between -1 and -5°C . Mobility is not restricted until -10 to -12°C in winter populations. Warm acclimatized groups select a mean ambient temperature of $+14^{\circ}\text{C}$ which closely parallels habitat temperature. The basis for this behavioral modification is the expanded range of operation of the central nervous system (Fig. 7) (Baust 1972). Nervous activity is terminated in the summer groups at 0°C . Mobility is impaired at $+4^{\circ}\text{C}$. Overwintering groups have nervous activity extended to -11°C due to differential fiber sensitivity and hence activity. During summer, two fiber units are apparent (Unit #1, activity range 15 to 29° ; Unit #2, 0 to 15°C) while in winter six units are operative (#1, 12 to 16° ; #2, 9 to 12° ; #3, 2 to 9° ; #4, -1 to 2° ; #5, -6 to -1° ; and #6, -11 to -6°C).

The gall fly, *Eurosta solidagensis*, is a temperate species ranging from southern Canada to northern Mexico at its extremes. It is freezing intolerant for all developmental stages except the overwintering third instar larvae. This species demonstrates a three phase cryoprotectant system based on the accumulation patterns of glycerol, sorbitol and trehalose. Accumulation of each component is initiated before freezing but may be related to cooling. Freezing encounters result in marked elevations in glycerol and sorbitol levels. Each protective component is diminished rapidly with spring warming (Fig. 8) (Morrissey and Baust 1976).

One paradoxical observation is noted. With peak cryoprotectant concentrations, SC's are elevated to temperatures above summer means. Apparently nucleator efficiency is enhanced to insure freezing. Third instar water content varies between 71 and 58% (August to January). The pupa compensates for occasional freezing exposures by extended supercooling to -23°C but without the benefit of protective agents.

Since trehalose levels increase up to $400\text{ mg}\%$ while glycerol and sorbitol to a lesser extent remain elevated in concentration, it is suggested that a source other than glycogen serves as a precursor. During a 30 day period between late summer and early autumn, glyceride and free fatty acid levels were monitored. Monoglycerides were not detected, diglyceride levels remained relatively constant but both triglyceride and free fatty acids decreased to 0% . This observation may indicate that lipids serve in addition to glycogen as a glycerol source.

A third species, *Coleomegilla maculata* provides yet another example of the diversity of overwintering strategies and the problems involved in inter-specific comparisons. *C. maculata*

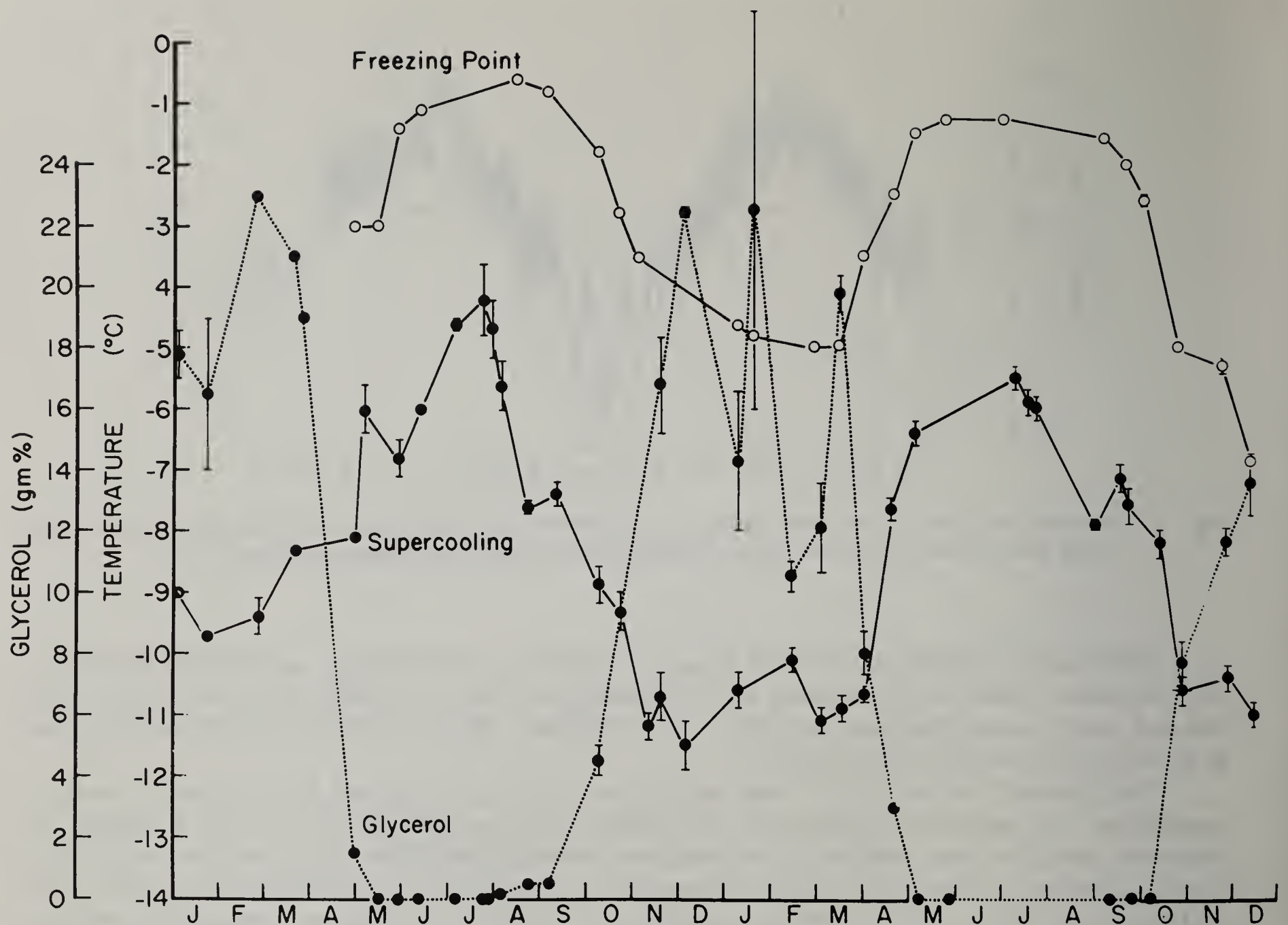


Fig. 4. — Seasonal variations in hemolymph glycerol content, supercooling and freezing points. Supercooling points are whole body determinations on *P. brevicornis*. Values are mean \pm S.E.

overwinters as an adult in aggregations that can approach 10^6 individuals and is freezing intolerant. Selected hibernacula remain exposed to ambient temperatures throughout the overwintering period.

This species provides an interesting profile. It does not synthesize an as yet identifiable cryoprotectant, maintains a constant water content and has developed the ability to “mask” nucleators resulting in an extension of mean SCp’s from a summer high of -6.0° to a winter low of -18.4°C (Baust and Morrissey 1975) (fig. 9, Table 2). Summer and winter populations demonstrate unimodal SCp distributions while spring and autumn groups are generally bimodal.

Laboratory acclimation experiments were conducted to evaluate the “masking” phenomenon. Outdoor specimens were warmed acutely to 25°C and maintained on either a diet of nucleator-free, distilled water (3X) (DW) or distilled water — 10% glucose (DWG). From the shift in SCp distribution pattern (Fig. 10), it is apparent that within 96 hours specimens on the DW diet underwent an equivalent six month seasonal transition whereas the DWG group demonstrated a more gradual transition to “summer” unimodality.

After 96 hours at 25°C , re-acclimation to 5°C was attempted (Fig. 11). The DW group did not re-acclimate but the DWG group underwent SCp changes equivalent to a mid-autumn state. Glucose is an efficient cryoprotectant and served as a nucleator mask during re-acclimation. Water content did not fluctuate nor correlate with changing SCp’s.

Discussion

The state of our knowledge regarding insect freezing tolerance is as best sketchy. A number of systems have been described to the extent that more questions are evident than are answered. The interspecific heterogeneity of the overwintering response make comparisons difficult. Even as

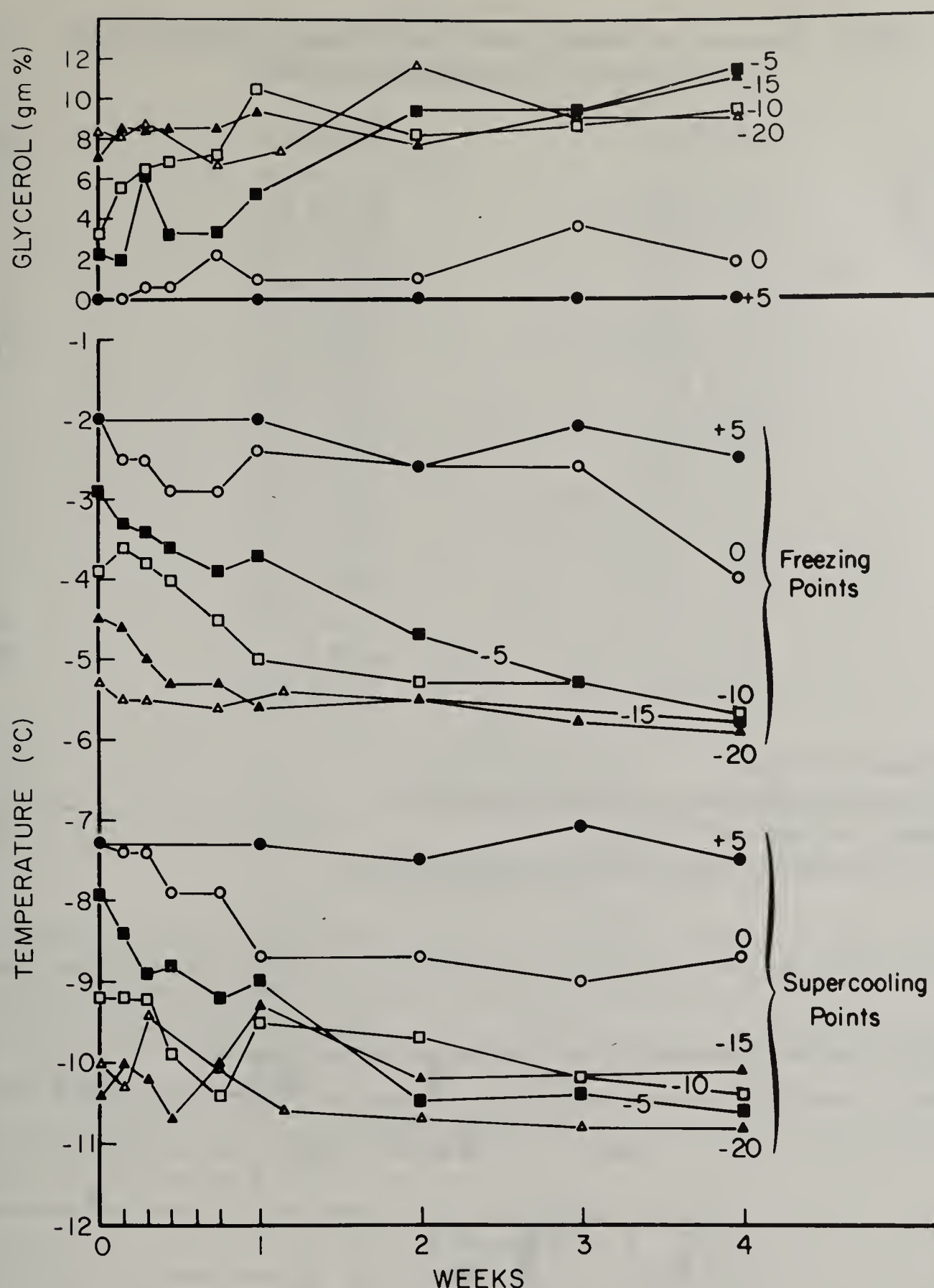


Fig. 5. – Variations in hemolymph glycerol content, freezing points and whole body supercooling points during autumn (low temperature) acclimation in *P. brevicornis* (Baust and Miller 1972).

“restricted” an adaptation as freezing tolerance is sufficiently diverse among the Insecta to preclude all but qualitative generalizations.

The presence of a polyhydric alcohol or low molecular weight carbohydrate in high concentrations is not essential for successful overwintering but is for freezing tolerance. Other categories of cryoprotectants may be identified in the future. Feeney (1974) and De Vries (1971) have identified a glycoprotein with biological “antifreeze” function in antarctic fish. While the glycoprotein offers little or no protection in the event of freezing, it does permit extended supercooling.

Exceptions to the normative overwintering patterns may exist. However, the few reported (Somme, 1964) may be subject to re-evaluation in light of current information. The basis of the re-assessment should be four fold. First, in which mode of protective function is the cryoprotectant acting: ice avoidance through extended supercooling or through the maintenance of critical intracellular and membrane fluidity in the presence of extracellular ice? Second and third, what is the threshold of cryoprotectant necessary for freezing tolerance and have the laboratory handling procedures permitted warm acclimation to proceed resulting in insufficient protective capacity?

Table 2.—Seasonal variations in mean supercooling points (SCp) and water content of *Coleomegilla maculata*.¹

Date	\bar{X} SC _p (°C)	\bar{X} % H ₂ O	Population ²
10/12	−13.4 ± 0.5	53.7 ± 1.3	A ³
10/29	−13.9 ± 0.7	50.3 ± 1.9	A
11/7	−15.7 ± 0.7	56.6 ± 2.9	A
11/29	−16.7 ± 0.6	56.8 ± 1.0	A
12/5	−17.2 ± 0.6	55.5 ± 1.6	A
12/11	−17.9 ± 0.8	55.0 ± 0.8	A
12/18	−18.4 ± 0.4	50.5 ± 0.9	A
12/28	−18.1 ± 0.4	53.9 ± 2.3	A
1/17	−17.8 ± 0.4	52.5 ± 0.8	A
2/7	−17.0 ± 1.1	62.3 ± 2.5	B
2/18	−16.7 ± 1.2	49.9 ± 1.3	C
3/6	− 8.5 ± 1.0	59.3 ± 1.6	D
April	− 5.5 ± 0.4	63.4 ±	Mixed ⁴
May	− 6.0 ± 0.2	62.7 ±	Mixed ⁴
July	− 6.3 ± 0.2	53.2 ± 1.6	E

¹ Values ± standard error of the mean.

² Population letters represent results, data from separate hibernacula.

³ Correlation coefficient for group A = 0.07.

⁴ Mixed represents a single monthly mean for non-overwintering groups.

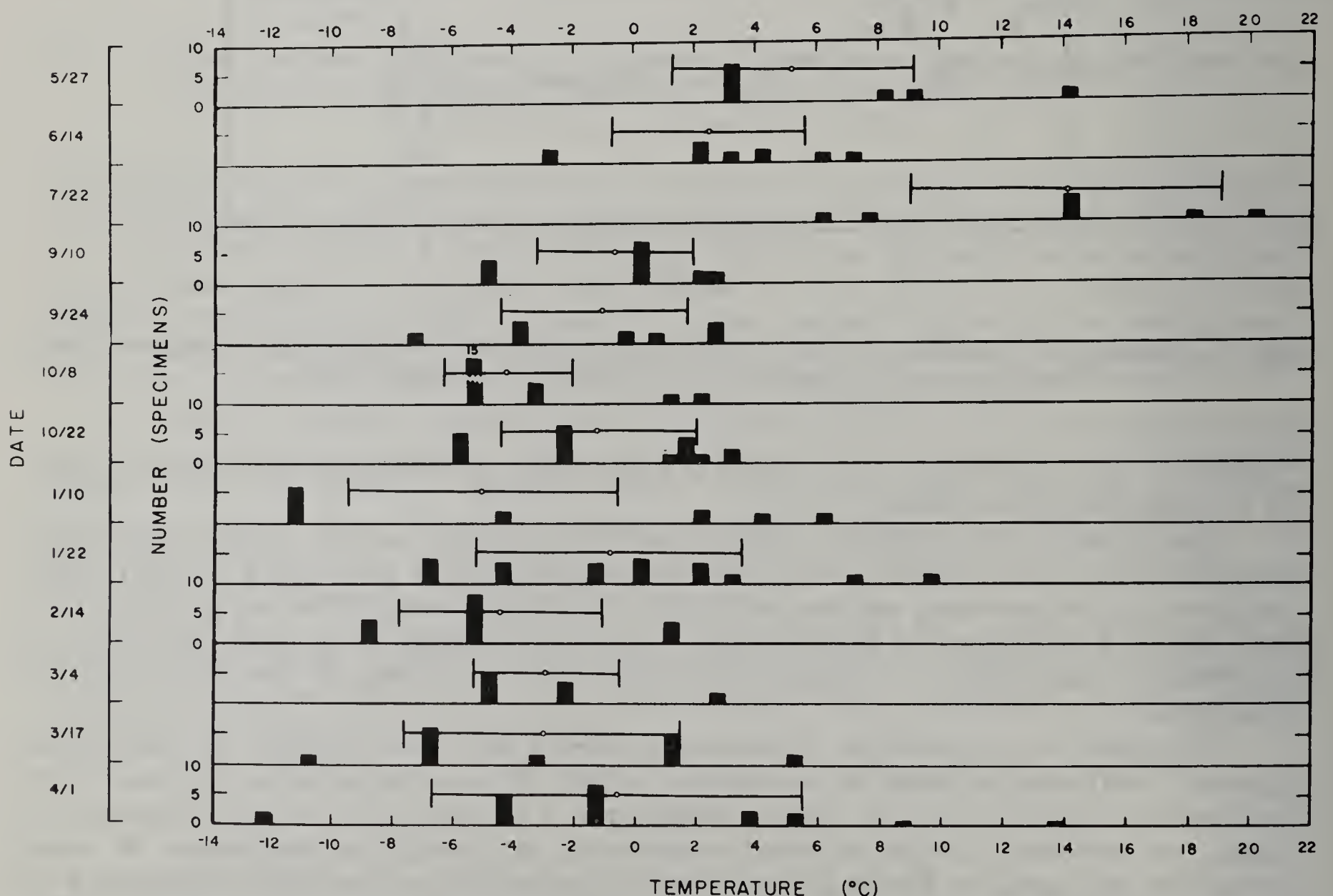


Fig. 6. — Annual variations in individual and mean temperature preferences demonstrated by *P. brevicornis*. Mean values are ± S.D. (Baust and Miller 1970).

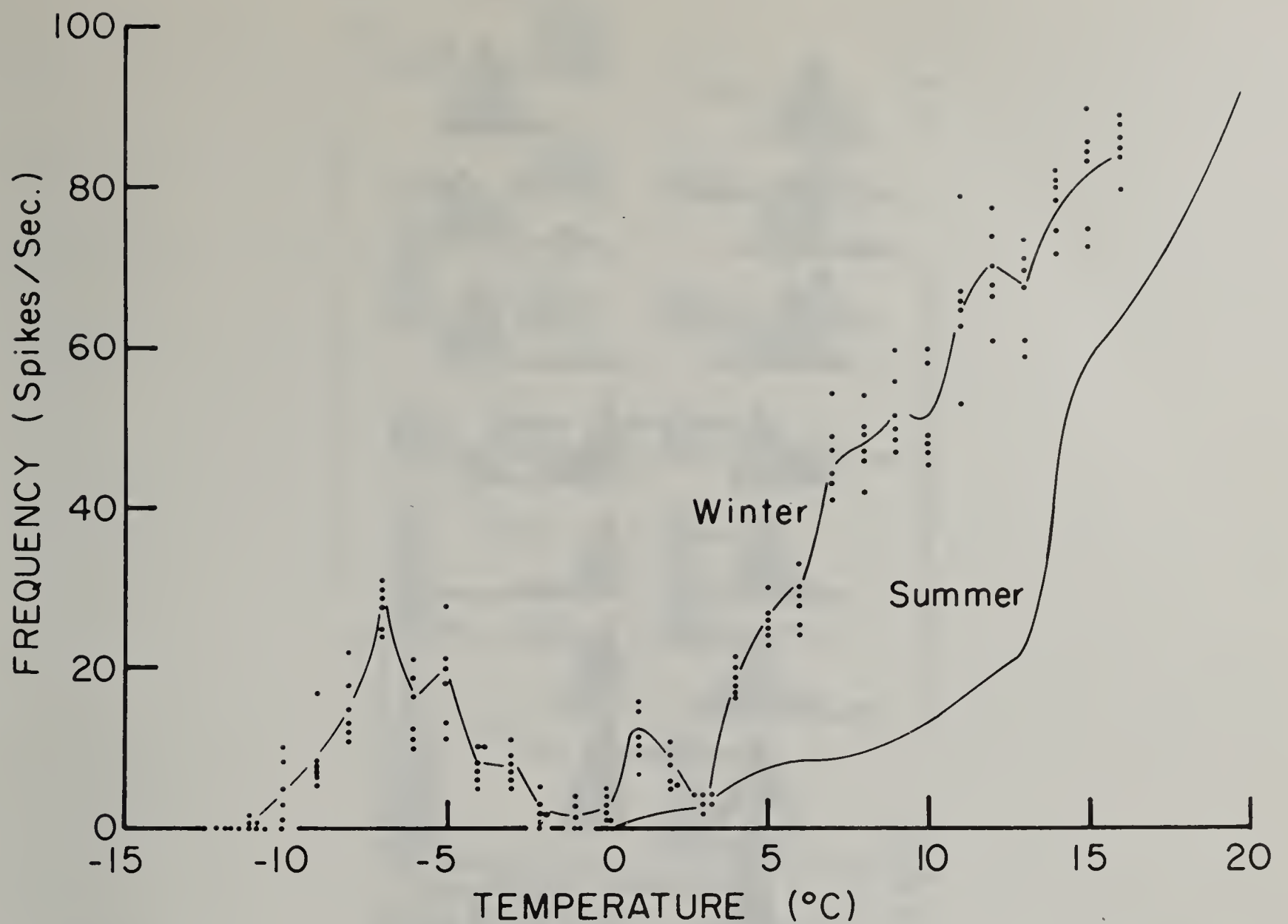


Fig. 7. – Dot frequency distribution and mean curve of motor neuron discharge vs. temperature in summer and winter acclimatized *P. brevicornis*. Six sample experiments are represented for winter specimens (·). Summer mean curve represents recordings from twenty specimens (Baust, 1972).

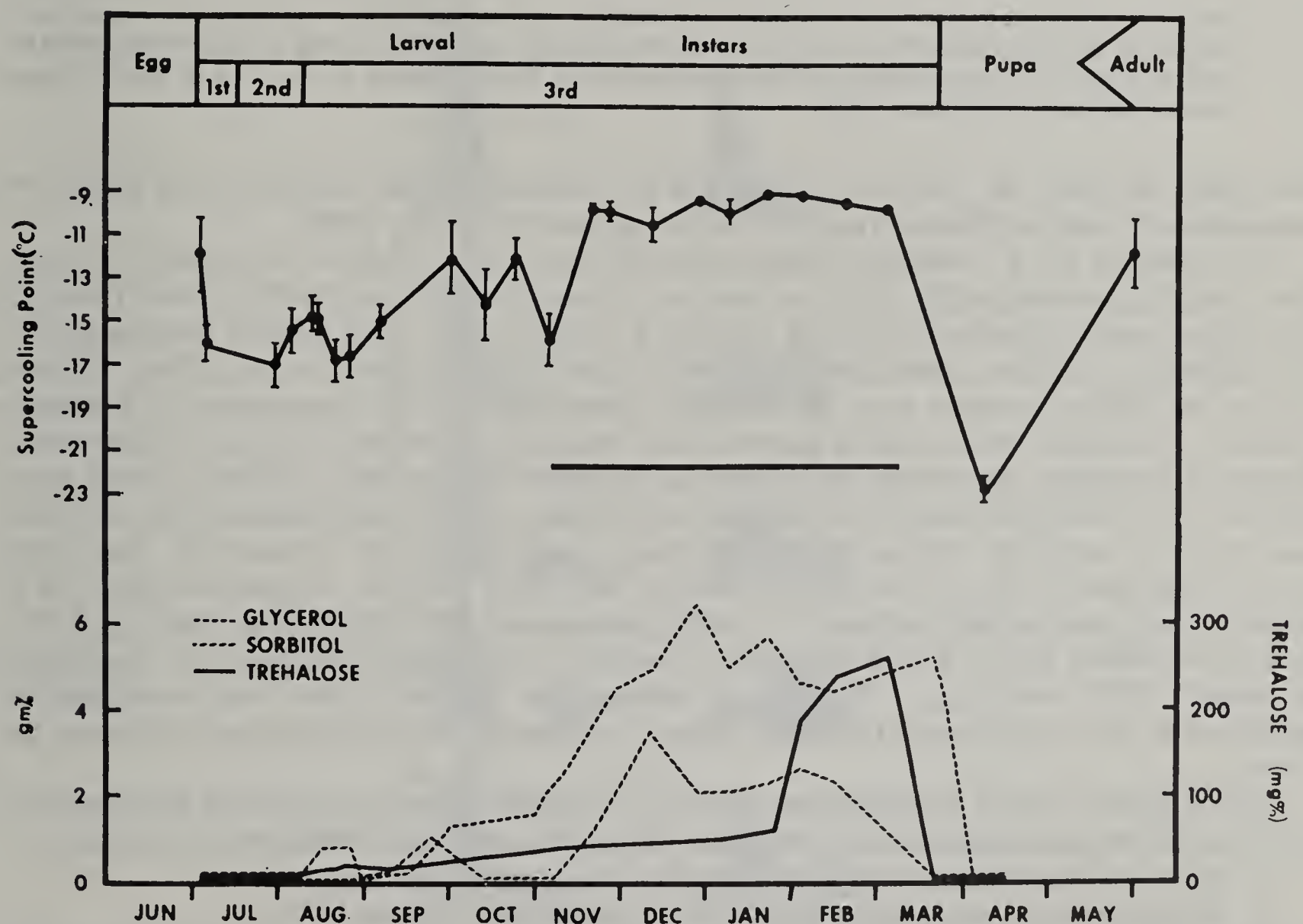


Fig. 8. – Seasonal variations in hemolymph cryoprotectant levels and whole body supercooling in *E. solidagensis*. The horizontal bar represents 90% survival after freezing (Morrissey and Baust 1975).

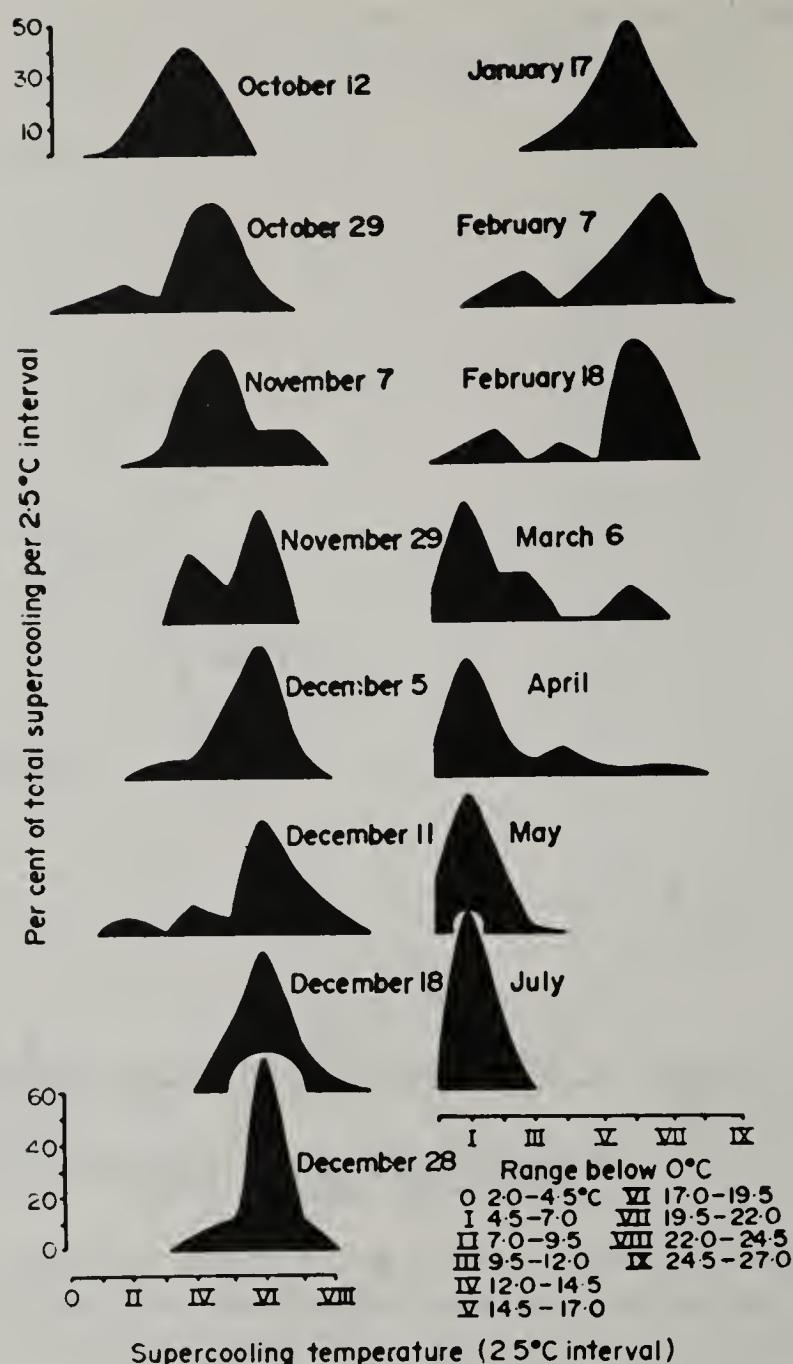


Fig. 9. — Frequency distribution curves of supercooling (freezing) temperatures of *C. maculata* over a yearly cycle. Specimens were collared at 1°C/min. Curves were smoothed by taking the running means of frequencies for each of five 0.5°C temperature intervals and correcting the mid-points of the tops of the histogram columns (Baust and Morrissey 1975).

Fourth, what has been the pattern of changes in low molecular weight carbohydrates? Mono- and disaccharides are rated as efficient cryoprotectants as glycerol (Doebbler 1966).

P. brevicornis and *E. solidagensis* demonstrate different freezing tolerant strategies. The former utilizes a single protectant while the latter relies on a three phase system. Careful review of the data indicates that nearly equivalent protective capacity is attained at the same ambient temperatures. In theory polyhydric alcohols offered protection due to their high hydrogen bonding affinity. That is, they have the ability to retain water in the liquid state at subfreezing temperatures. A qualitative assessment of protective action can be pictured as a “hydroxyl equivalent”. The greater the number of hydroxyl terminals, the greater the number of hydrogen binding sites available to hold water molecules. If *P. brevicornis* and *E. solidagensis* are compared at the same temperature, -20°C (the lowest exposure naturally experienced by the study population of *E. solidagensis*), the “mean hydroxyl equivalents” (\bar{E}_{OH}) are nearly identical but with different cryoprotectants. For *P. brevicornis*, with glycerol levels between 9.5 gm% (autumn) and 10.5 gm% (spring), the $\bar{E}_{OH} = 29.5$. During a two month winter period (December–January) when ambient temperatures consistently drop below -20°C, the $\bar{E}_{OH} = 31.5$ for *E. solidagensis*. Therefore, the total cryoprotectant contribution to each species must be viewed before a conclusion on the mechanism of tolerance can be drawn.

In conclusion, a list of generalizations based on data obtained from three species is presented. It is hoped that these observations serve to stimulate further discussion and investigation in this area.

1. Insects may overwinter in any developmental stage (species specific).
2. Habitat selection may provide clues to the tolerance limits (Baust 1976).
3. Temperature preference may vary seasonally. Specimens may even actively select sub-freezing exposures in order to avoid transient and potentially lethal warm acclimatization.

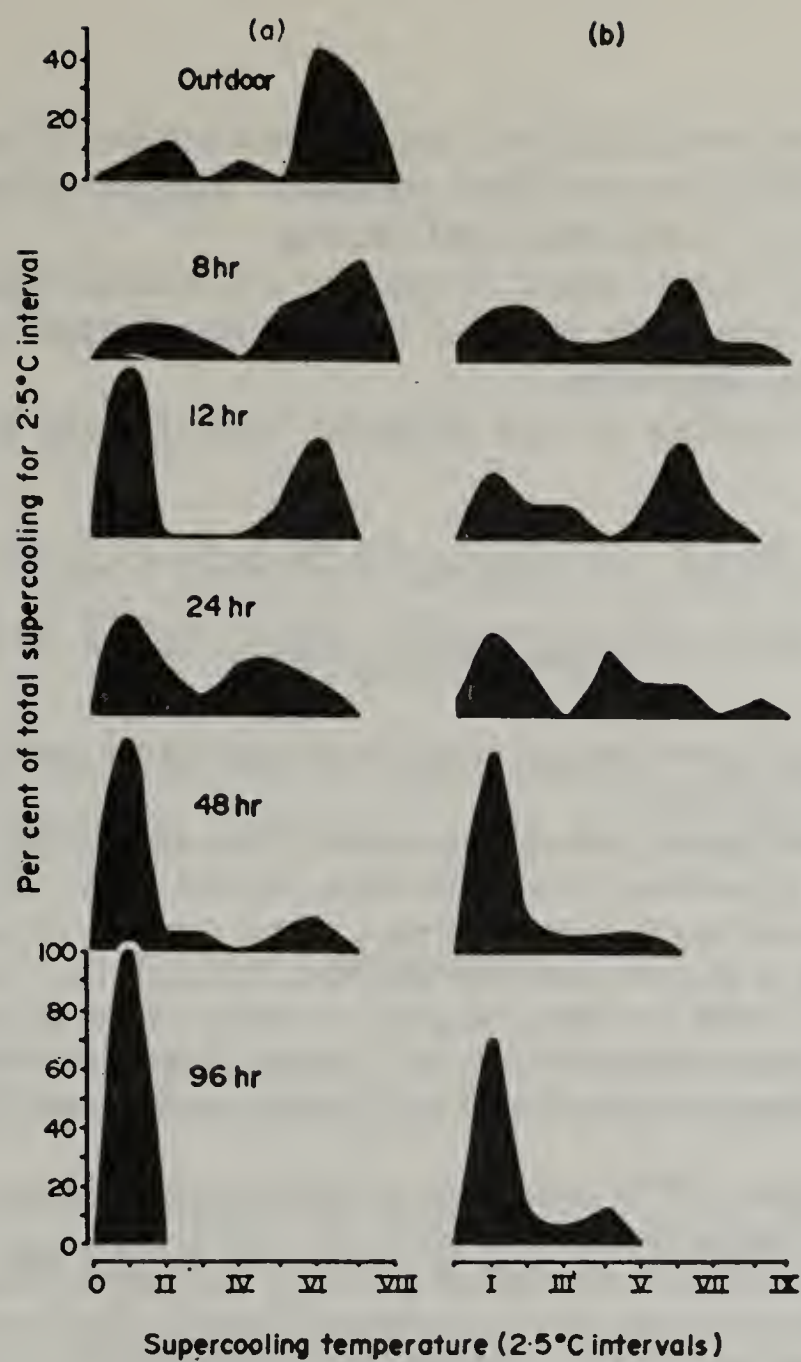


Fig. 10. – Frequency distribution curves of supercooling temperatures of *C. maculata* during warm acclimation, (25°C). A = distilled water diet; B = 10% glucose diet. Refer to figure 10 for specifics of curve preparation (Baust and Morrissey 1975).

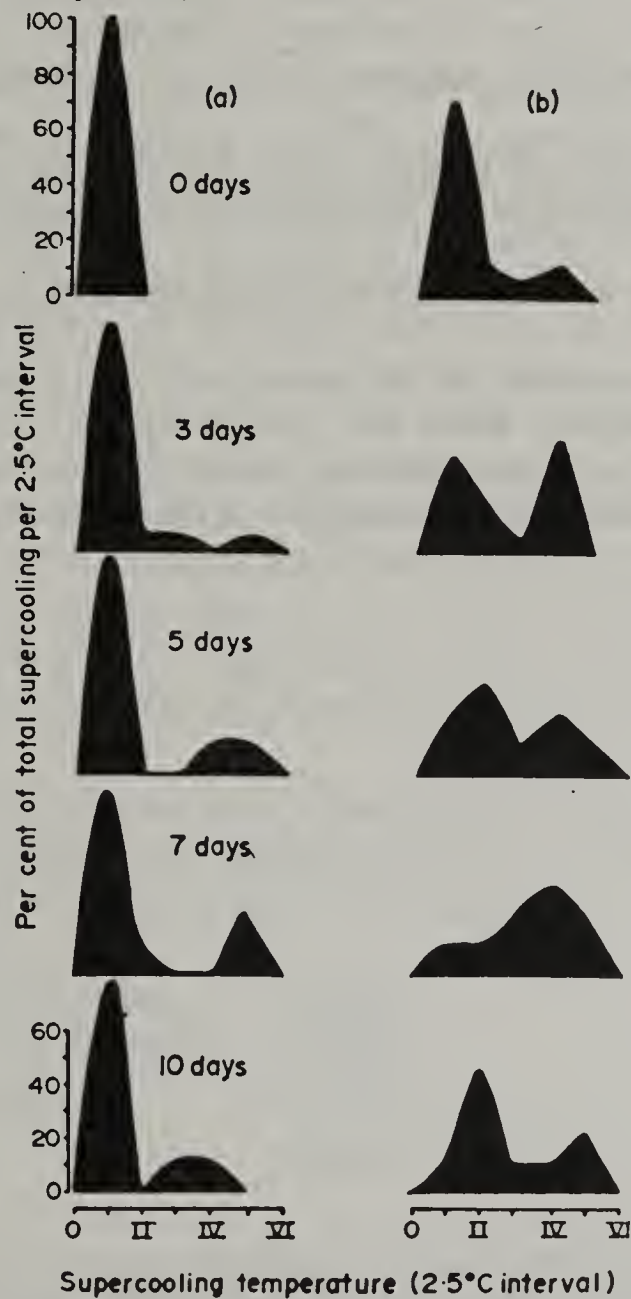


Fig. 11. – Frequency distribution curves of supercooling temperatures of *C. maculata* during cold acclimation (5°C). A = distilled water diet; B = 10% glucose diet. Refer to figure 10 for specifics of curve preparation (Baust and Morrissey 1975).

4. Physiological and biochemical activity may proceed at sub-zero temperatures and even in the frozen state. Kaufmann (1971) has described continued digestive processes at -40°C . Also, egg development is not initiated in *P. brevicornis* until freezing.
5. Seasonal variations in water content, if apparent, are of little relation to frost hardening.
6. The presence of a cryoprotectant is an insufficient criterion to draw conclusions on the mechanism of low temperature adaptation.
7. Casual laboratory handling of cold hardened specimens can lead to "irreversible" warm acclimation within hours.

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Altitude-and Time-related Changes in Arthropod Faunation (Central High Alps: Obergurgl-area, Tyrol)¹

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ABSTRACT

Some results of a still continuing year round project work from 1974/75 on changes of fauna with altitude (and time resp.) are given, exemplified by Oribatei and Coleoptera on the species level, otherwise by higher taxa.

The study area is near Obergurgl (1958 m) at the head of the Ötztal, about 60 km in a beeline WSW from Innsbruck, in the Central Alps. Climate is pronouncedly inner-alpine continental. Some soil data are given.

Investigations cover an altitude span of more than 1100 m, from manured meadows (1960 m) through the different life-zones till 3100 m (subnival).

Sampling by pitfall- and photo-elector-trapping, and by soil sample-extraction (Tullgren), allowing relative and absolute quantitative estimates, delivered a total of about 111,000 specimens. Conversions to biomass are not yet made.

Comparisons mainly concentrate on intensive sites (valley meadows, 1960–1980 m; *Curvuletum*, 2650 m). They concern seasonal changes as well as changes with altitude of individual and species numbers, dominance structure, diversity (Shannon-index), similarity (Sørensen-quotient).

Preliminary production-estimates by means of time period-sorted photo-elector-data are in the mean about 1.9 times larger in the manured wet meadow (1980 m) as in the *Curvuletum* (2650 m).

But approaching to end of season the alpine site-value can nearly become 3 times larger. During periods with peak activity values of both sites are of the same order. From values for Oribatei could be concluded, that the alpine site is superior over the valley meadow by about 4 times in the mean.

Since 1974 a team of scientists and students of the Zoological Institute, University of Innsbruck, has worked in the Central Alps of Tyrol to gain some insight into invertebrate high alpine terrestrial ecosystems. Some of the investigations will simultaneously deliver the necessary base for zoological research, which has to be done by us in the frame of the "MAB-6-Gesamtvorhaben Obergurgl" (see Bunnell et al. 1974. W. Møser and M. Møser, 1975). Within this Man and Biosphere project the alterations of these ecosystems by touristic use of the landscape (like skiing etc.) are to be investigated.

The aim of this talk is to present some selected first results from our field work in 1974 and 1975. It began mid-July 1974 and is still going on. We will concentrate mostly on data from 1975. Comparisons with results from elsewhere will not be made yet.

Information is based on:

- | | |
|--|---------|
| 1. Pitfall-traps; sum of individuals: | 68,000 |
| 2. Photo-electors; sum of individuals: | 18,600 |
| 3. Oribatei from soil samples: | 24,300 |
| | <hr/> |
| | 110,900 |

¹Contribution No. 1 of the project "Jahreszyklus und Massenwechsel in terrestrischen Hochgebirgszoozönosen". Supported by the Austrian "Fonds zur Förderung der wissenschaftlichen Forschung", Projekt-Nr. 2336.

4. Coleoptera from 1+2: 17,300.

The research area is situated about 60 km on a bee-line WSW of Innsbruck in Tyrol on the WSW-exposed mountain-slopes at the end of the Ötztal near the village Obergurgl (1930 m). This area belongs to the old crystalline of the Ötztal mass and is situated in the core of the inner-alpine continental climate, characterized by low precipitation, low cloudiness and strong temperature oscillations.

Selected data from the Obergurgl observation station (1950 m) are: Global radiation for the year (period 1957-63): $114052 \text{ cal.cm}^{-2}.\text{d}^{-1}$; number of days/year with freezing temperatures 203,6; abs. max. air temperature $+25.8^{\circ}\text{C}$, abs. minimum -30.6°C (period 1953-60) annual mean 2.2. (H. Schatz, 1976: Physiographie von Obergurgl; unpubl. MS., compiled for the project purposes). For some summarized information see Leising (1976) and Schedl (1976).

Investigation sites rise in steps through the different life-zones from two manured meadows at the valley floor (1960-1980 m) (W,M), and a *Pinus cembra* forest (2070 m) (Z), dwarf-shrubs and extended lichen-heaths (2100-2400 m) (F,T1-4), alpine meadows (2500-2650 m) (T5-6,R), up to the subnival life-zone (2800-3100 m) (L), with intensive sites meadow "W" (1980 m) and "M" (1960 m) and "Curvuletum Rosskar" (2650 m) (R). The other 9 form a vertical "transect" for extensive studies (F, T1-6, L).

Details on climate, microclimate, vegetation, and soils will be published elsewhere. During the observation time weather differed considerably from the long-term means. Especially precipitation was distinctly lower in 1974 with 719 mm/year and in 1975 with 990 mm/year much higher than the long-period mean of 807 mm/year (Obergurgl station, 1950 m). At the end of August, 1975 there were strong temperature falls with heavy snow, causing snow cover of 40 cm at the intensive station Rosskar and a drop of the temporary snow line to 2200 m for about a week, and influencing strongly arthropod activities at the soil surface and in the vegetation strata. These depressions can easily be recognized in the diagrams of variation with time.

Soil-types, very simplified, are as follows (Tab. 1): The two meadows have different brown soils, the *Pinus cembra* forest iron podsol, the extrasilvatic dwarf-shrubs podsolranker (T1) and degenerated iron-podsol respectively (T2), the lichen-heaths degenerated iron humus podsol (F), a well developed iron humus podsol (T3), or a shallow iron humus podsol (T4, T5). The latter also in the alpine meadow (T6). In the intensive station R (Curvuletum, Rosskar, 2650 m) there are different alpine "Rasenbraunderden" (R_1), partly "pseudovergleyt" with signs of podsolisation.

Table 1 shows some pedologic characteristics from selected sites as pore space, water capacity, air capacity, content of organic substances, and pH. Only the data from the "upper soil" (horizons L, O, A) are given here.

Vegetation and soils form a very complicated small scale mosaic pattern whereby the influence of the relief and the convexities and concavities of the surface increase with altitude.

At the moment we will not try to analyze observed variations of the fauna with altitude or time of the year by relating them with single selected parameters. Our data processing with the necessary computer aided statistics has not gone so far yet. We will only relate with vegetation, which is indicative for mean environmental conditions.

Changes with Altitude and Vegetation-belts Respectively

Fig. 1 gives a generalized overview of the representation of dominant arthropod groups by pitfall-trapping during the vegetation period June-October 1975. Circles W and M represent respectively a "wet" meadow (W) and the rather dry one (M) as intensive stations of investigation. Z means the very complex intrasilvatic dwarf-shrub in the uppermost *Pinus cembra* forest, T1-T6 means the transect: T1 and T2 are extrasilvatic dwarf-shrubs, T3 and T4 are from the extended lichen-heaths belt, T5 is a stony alpine meadow (*Curvuletum*), T6 and R high alpine meadows (*Curvuletum*), whereby R is our intensive station Rosskar, 2650 m. L. symbolizes "Liebener Rippe," a ridge in the subnival life-zone with cushion plants, cryptogams, and fragments of alpine meadows. Investigations there have been made from about 2800-3100 m. This ridge was still a nunatak, surrounded by glaciers, in the middle of the past century. In consequence of the retreat of the glaciers later on, it is now in communication with the lower areas. An access to this site is made dangerous by avalanches out of the short vegetation period. Therefore the number of trapping periods (4) is less than at the other sites, and the time considered in the diagram is from September 1974 till October 1975, instead

Table 1.—Selected Parameters of the Uppersoil in some investigation sites.
 Horizon-symbols following the FAO-recommendations.
 (After unpublished data by Dr. I. Neuwinger and H. Passecker, Innsbruck).

Horizont	Machtig= keit (cm)	HV	PV	Wasserkapazität +)		Luftkapazität		pH	O.S. (G.%)
				WK _{max}	FK	WK _{max}	FK		
W 1980m. Feuchtwiese:									
A _h	(10)12	100/120	75/90	67/80	66/79	8/10	9/11	4,7	30-40
AB _g	20	100/200	63/126	51/102	47/94	12/24	16/32	4,0	8-10
1. Bodentyp: pseudovergleyte podsolige Braunerde auf Podsolkolluvium. 2. Bodenart: lehmiger Sand. 3. Humusform: Mull.									

M (MAB ₁) 1960m. Magerwiese:									
(L/O) /A _{h1}	2	100/200	75/15	—	—	—	—	4,3	37
A _{h2}	12	100/120	74/89	70/84	50-60/ 60-75	30/36	14/24/ 14-29	4,3	8,5
A _{h2} /B	15	100/150	66/99	55/83	40-50/ 60-75	45/67	16-26/ 24-39	4,3	8,2
1. podsolige Braunerde auf Podsolkolluvium. 2. lehmiger Sand. 3. Mull.									

Z (Z ₁) Zirbenwald, 207m. Vergaste Alpenrosen-Beerenheide:									
O _f	6	100/60	80/48	67/40	40/24	13/8	40/24	3,5	>50
O _h	4	100/40	80/32	67/27	40/16	13/5	40/16	3,4	>50
A _e =E	(3)6	100/60	66/40	56/34	45/27	10/6	21/13	3,7	5-10
1. Durch Beweidung and Erosion gestorter Eisenpodsol, pseudovergleyt. 2. Steniger Sand. 3. Rohhumus.									

T1 (T _{1B}), 2100m. Dichte, moosreiche Alpenrosenheide:									
O _f	(2)3	100/30	80/24	—	—	—	—	3,5	>50
O _f /h	20	100/200	80/160	32/64	19/38	48/96	—	3,4	>30
R=C									
1. Podsolranker. 2. Schutt mit Grobsand. 3. Rohhumus.									

T4 2400m. Loiseleurietum:									
L/O _f	(4)5	100/40	80/40	75/38	35/18	5/2	45/22	3,9	>50
O _h	20	100/2000	77/160	52/104	25/50	25/16	52/110	3,8	>50
1. flachgrundiger Eisenhumuspodol. 2. steniger Sand. 3. Rohhumus.									

R (R ₁) R0Bkar, 2650m. Curvuletum:									
L	2,5-2	100/5	80/4	75/3	40/2	5/0,2	40/2	3,9	54
O _h	2-0	100/20	75/15	70/14	38/8	5/1	37/7	3,9	35
A _h	0-5	100/50	73/36	66/33	36/18	7/3	37/18	3,8	25
(E)	5-6	1000/10	—	—	—	—	—	3,7	19
1. schwach podsolierte flachgrundige Braunerde. 2. stark steniger Sand. 3. Rohhumus.									

+) WK_{max}=maximale Wassersattigung (0,01 at Saugspannung)

of June to October 1975 at all the other sites. At the latter the traps were emptied fortnightly during the vegetation period.

The systematic groups represented with more than 3% are graphed. The diameter of the circles i.e. the mean catch at the site per sample unit is related to the sum of the mean catches of all sites. Therefore these reduced data make activity densities at the different sites directly comparable. Hence, catches have been most effective in the down-valley and high alpine meadows. The diversity of systematic groups decreases with increasing altitude, as was to be expected (e.g. see Janetschek 1973). This could best be seen by differentiating the integrated remaining groups, which include in M + W 11 arthropod groups + Lumbricidae and Gastropoda; in R 5 arthropod groups, where Lumbricidae have disappeared (they were still present in the pitfall-trappings in T5); and in L lastly only Gastropoda, Opiliones and Lepidoptera were caught by this method, besides the signed groups. Diptera are the predominant group except in the dwarf-shrubs (Z, T1, T2); their dominance increases with increasing altitude. Maybe this is a special effect of the pitfall-trapping-method, since the dwarf-shrubs with *Juniperus*, *Rhododendron*, and *Vaccinium* give a good wind shelter and small flying insects have no need to stick near to the soil surface, whereas the low vegetation of the lichenheaths, *Loiseleurietum* and *Curvuletum*, does not offer such a wind shelter. Flying insects here keep near to the soil surface and flight activity binds to change to crawling at the surface. The pitfall-trapping therefore seems to be a very effective method for catching certain small flying insects under more extreme environmental conditions. Otherwise, as shown by the photo-elector-method, which gives absolute estimates for flying insects, the percentage of Diptera also increases with increasing altitude as is shown by the comparison of the intensive sites (M, W, R), where that method has only been used (Fig. 2). Actually, small Diptera (Lycoriidae a.o.) were found predominantly in the pitfall in the centre of the photo-elector, and less in the box at its top.

Spiders are the most dominant group in the dwarf-shrubs, especially in the intrasilvatic one; their proportion decreases in the lichenheaths and the *Curvuletum* and is in R of the same size as in the dry meadow M. In the subnival site (L) their proportion increases to the same order as in the upper extrasilvatic dwarf-shrubs. The proportion of Coleoptera is high in the valley meadows and the dwarf-shrubs and becomes small in the upper life-zones.

The large percentage at site T2 (upper extrasilvatic dwarf-shrub) is the consequence of mass-appearance of two small Staphylinids (*Liogluta nitidiuscula* Sharp. and *Atheta leonhardi* Bh.), which have possibly found optimal life conditions here. We have to wait for results of the following years. Also the Opiliones decrease with increasing altitude, whereby the species *Mitopus morio* was by far dominant (but trapped only up to T4). The large percentage of Hymenoptera in the pitfalls in R is surprising. Essentially it concerns small parasitic forms. But photo-elector results in R (Fig. 2) are exactly the same in terms of percentage as the pitfall-results, and in the valley meadows of the same order of size as in R, whereas pitfall % in W and M are very small. Therefore, the same behaviour as discussed earlier for small Diptera could be responsible for the effectiveness of pitfalls in R too. Diplopoda appear only at sites with sufficient litter, therefore especially in the dwarf-shrub zone. Thereby it had to be taken into consideration that they start to move and get trapped only with the third stage.

It should be mentioned that the site T5 (stony *Curvuletum*) seems to offer good life conditions for the Diplopod *Trimerophorella nivicomis* Verhoeffi, a zoogeographically very interesting endemic species of the middle central Alps, which is claimed to be a nunatak-relict. Adult specimens have been trapped in T3 up to T6. But only in T5 also *inadulti* (5.-6. stage) have been found in the traps.

Fig. 2 shows the dominance structure of higher taxa, resulting from emergence trapping with photo-electors at the intensive sites. The given numbers of individuals/m² means the sum over the whole operating time = (total catch/number of traps) x 4. Operating time roughly corresponding with snow-free time (vegetation-period) was shorter in the dry meadow M (91 days) as in the otherwise comparable wet meadow W (141 days). Therefore the value for M (=2300/m²) is not given in the graph and cannot be compared with the others. This method should allow estimates of production. We will discuss that briefly at the end of the talk.

The sequence of the seasonal mean of dominance is the same in all three sites: 1. Diptera, 2. Hymenoptera, 3. Coleoptera, 4. Arachnida. But between the Diptera there is a clear increase of Nematocera with altitude. Altogether the structure of the valley meadows resembles very much that of the high alpine meadow. Nevertheless individual-production is obviously higher in the valley meadow W than in the high alpine meadow (comparing the values of the graph, 2.4 times larger). This method seems to have the disadvantage that possibly certain forms are underrepresented, because

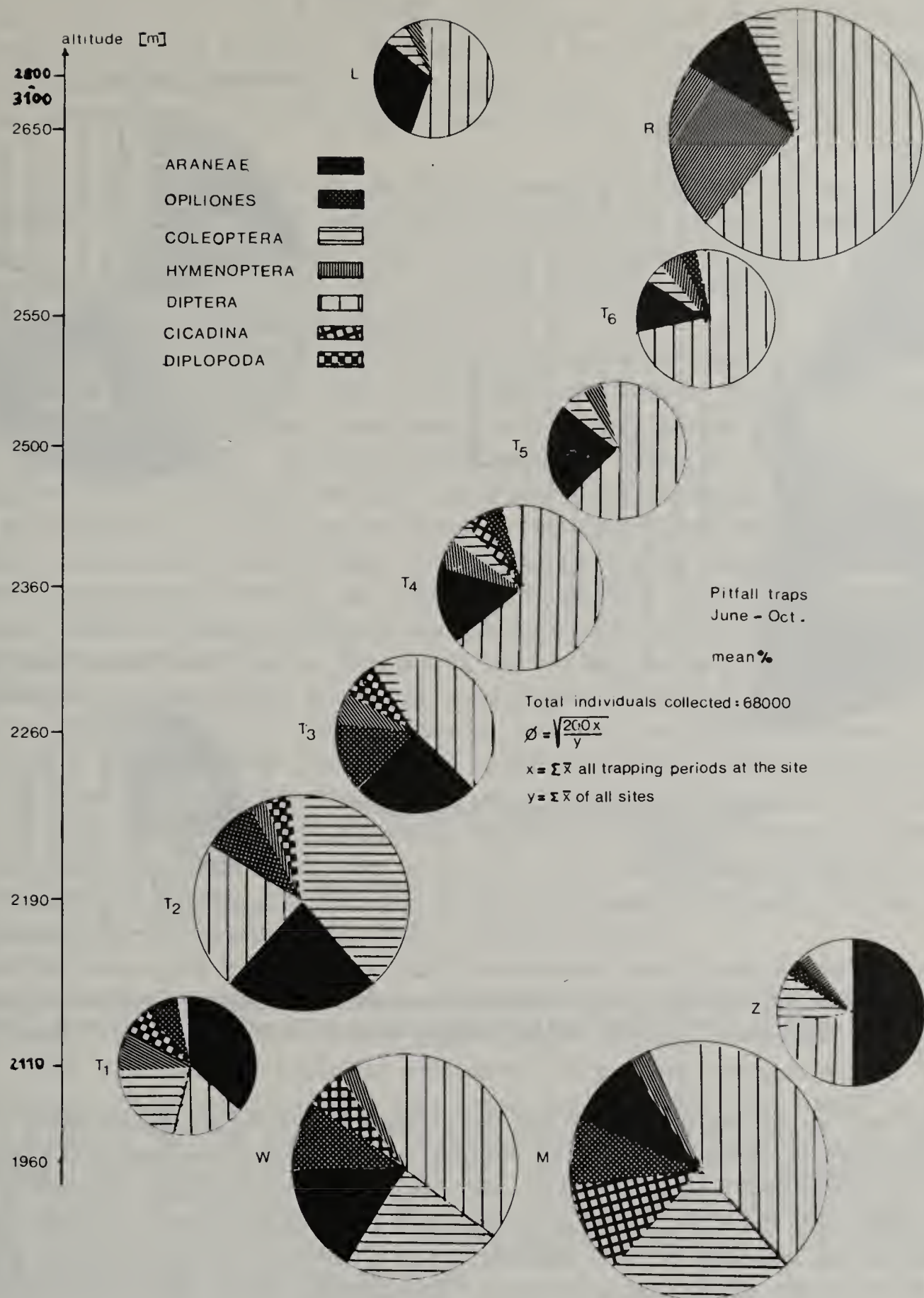


Fig. 1. — Percentages of higher taxa in the investigation sites, based on pitfall-trappings during the season June to October 1975.

Graphed are groups with $>3\%$, with the mean % at the respective site over the above period. In L (2800-3100 m) also data from September 1974 are included.

On account of differing numbers of traps, data are reduced, so that diameters of circles give a direct comparable estimate of the different activity-densities.

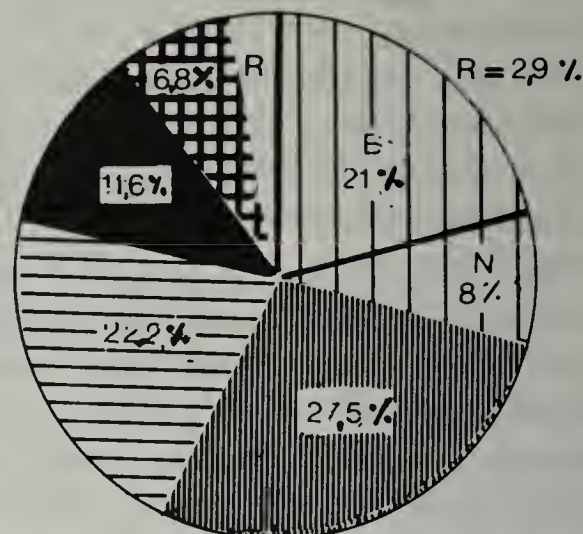
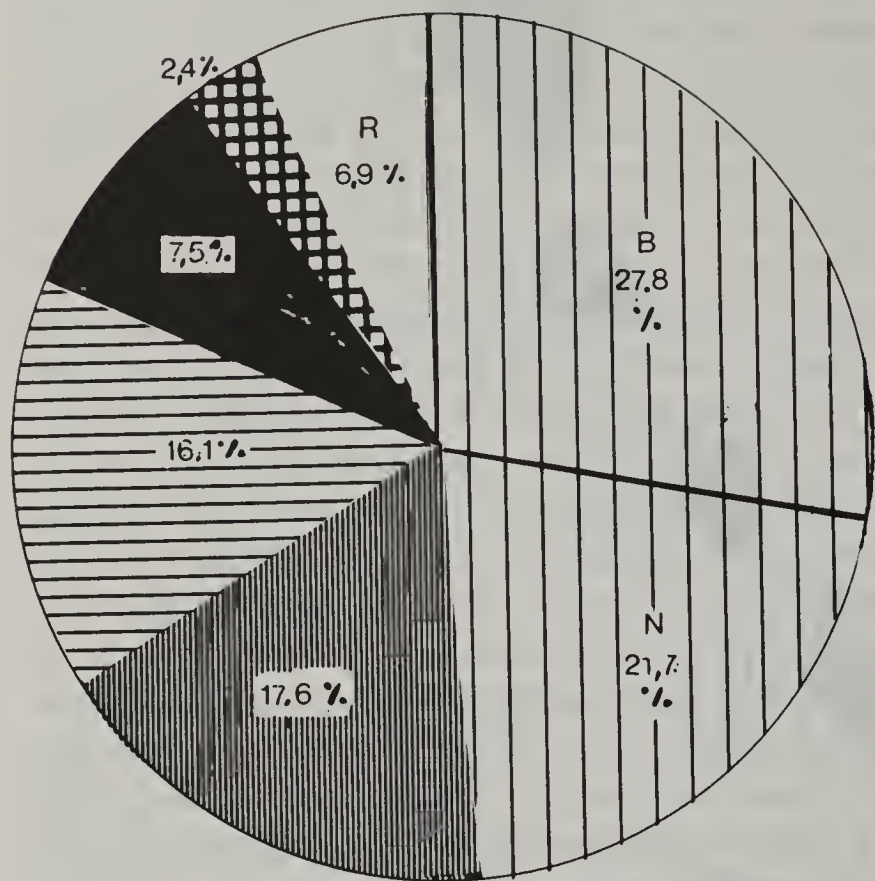
Numbers of traps were: in M, W, and R 20 each, in Z 16, in T1 — 6 7 each, in L 6. Emptying 2-weekly during the vegetation period, in L not at regular terms. Trap-liquid was K_2CrO_7 (in 1974 formaline). For relation of sites to life-zones see Figs. 3-6.

The not differentiated rest ($<3\%$) includes:

Lumbricidae (M, W, Z, T1-5), Gastropoda (all sites, except T4, 6, R), Pseudoscorpiones (T5, 6), Opiliones (T6, R, L), Chilopoda (all, except T4, 6, L), Diplopoda (M, W, T4-6), Plecoptera (M, T4-6), Saltatoria (M, W, Z, T2, 3, 6), Thysanoptera (M, W, T2, R), Heteroptera (M, W, Z, T1, 2), Cicadina (Auchenorrh.) (T1-3, 5), Aphidoidea (M, W, Z, T5, R), Coccoidea (W, Z, T1), Neuroptera (M, T4, 5), Mecoptera (M, W, Z, T1, 2), Trichoptera (T3), Lepidoptera (all, except T6).

Meadow W (1980m) : 3840 ind./m²

Meadow M (1960m)



B = Brachycera
N = Nematocera
R = Rest

Total individuals collected 1975 = 18600

$$\phi = \sqrt{\frac{100x}{y}}$$

Alpine Meadow R (2650m) [Caricetum curvulae]: 1602 ind./m²

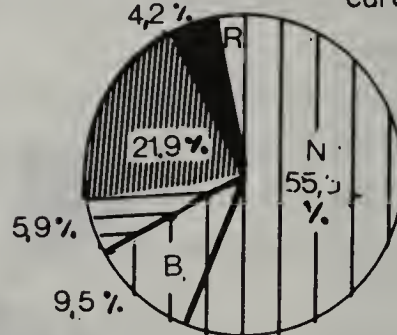


Fig. 2.— Percentages of higher taxa in the emergence-trap-catches at the intensive stations wet meadow, 1980 m (W), “dry” meadow, 1960 m (M), and high-alpine meadow, Curvuletum, 2650 m (R), by photo-electors, 1975.

Graphed are the annual mean % at the sites. Diameter of circles allows direct comparisons of each total catch (see explanation to Fig. 1). Number of photo-electors (with $f=0.25\text{m}^2$, and a pitfall trap in its center to reduce predation and to catch surface-specimens) were: 10 each in W and M, 8 in R. Operating time in M (91 days) was shorter than in W (141) and did not cover the whole vegetation period. Therefore the quantity of total individuals ($2312/\text{m}^2$) is not inserted in the graph. Operating in R (59 d) did cover the whole season, except an interruption, due to wild weather (see explanations to Fig. 10).

The not graphed rest (<2%) includes: Thysanoptera and Diplopoda (M), Lepidoptera, Diptera- and Lepidoptera-larvae, Heteroptera.

Operating terms of the traps see explanation to Fig. 10.

they may have a pupation niche, which is not covered by the method so that the emerged adults are not trapped. The pronounced similarity between valley and alpine meadows only holds for a high taxonomic level. Considering the species level, relations are different (see later).

Changes of individual- and species-numbers, dominance structures, similarity, and diversity with altitude, exemplified by Coleoptera and Oribatei. — Until now we discussed the understone- and vegetation assemblage of higher taxa as a whole (as it results from the methods used!). Results on the species level will be exemplified by Coleoptera and, as representatives of the soil-mesofauna, Oribatei. Altogether there are determined from the 12 sites at present: 139 species of Coleoptera (more than 17300 ind.; 13108 adults, 4210 larvae), not included 12 further species to be revised. Eighty-one species of Oribatei (more than 24300 ind.; 14074 adults, 10240 nymphs). The list is yet complete. For the Coleoptera only adults are considered on the species level. Determinations of larvae have not gone so far yet.

Sampling of Oribatei was done as follows: Soil samples of 11 cm² surface and 2 cm depth taken from three horizons (0-2, 2-8, >8 cm) were extracted in small Tullgren-funnels for 10 days (without treating). Sampling times and terms are different: In W since July 1974, 2-3 weekly during the vegetation-period, monthly winterover (snowcover being up to 2 m depth). In M since July 1975 with the same terms. In Z since July 1974 with the same terms as in W and M, but winterover only sometimes.

In R since August 1974, 2-4 weekly during the season, sometimes in winter. In F and L since July 1974, during the season 2-3 (in L 3-4)-weekly. In T1-T6 since June 1975, during the season 2-3 weekly. Altogether a total of more than 1600 samples was achieved. Oribatids concentrate in the uppermost investigation level (0-2 cm), that means in the litter and uppermost upper-soil. Their density in levels below 2 cm was generally negligible.

In Fig. 3 data on individual- and species-numbers and diversity are plotted for Coleoptera and Oribatei at the different sites. There are some heavy oscillations. Neglecting those obviously exceptional data, ocularly smoothed trend-lines were made, which may give a better (but schematized) impression of the altitude/vegetation-related changes in the above population parameters. The different oscillations are not yet understood in detail. Possible sampling errors cannot yet be excluded and it would need an enormous amount of field work to make allowance for the very complex small scale mosaic pattern of environments. This may especially be true for the Oribatids. Some explanations, however, are possible: The peak in Coleoptera abundance in T2 was already mentioned earlier as being responsible for the high total of that site (see Fig. 1). It is caused by the mass-appearance of two species. Neglecting this value, abundances are largest in the valley meadows, are of about the same size in dwarf-shrubs and the *Curvuletum* R, and are lowest in the transition-zone from lichen-heaths to alpine meadows, and in the subnival site respectively. Numbers of Coleoptera species show a similar trend line: a constant decrease with increasing altitude. If we summarize the species from both meadows, the drop is still more pronounced, from 106 to 8 (see Table 2). Therefore the diversity also (measured by the Shannon-Index) decreases rather regularly. It is highest in the meadows because of the high number of species, since the equitability component of $H(S)$ rather increases with altitude. The Shannon-Index would reach the maximum value, if all species had the same abundance. For details of that index see Krebs (1972).

Oribatei differ somewhat from beetles: High abundances were found in the lower extrasilvatic dwarf-shrub (T1), the alpine meadow R, and in one lichen-heath site (T3). These sites have in common the humus form (raw humus) with high values of organic substances (mostly above 50 weight %) (see Table 1). From the maximum abundance (T1) corresponds with a "Ranker"-soil under a *Rhodoretum* rich in mosses! Values were low in the meadows (with "Mull" as humus form, but a small air capacity, and less content of organic substances), in T2 and F (the transition-zone between vegetation-belts) and in the highmost site (L). That value is of the same order as that from the "dry" valley meadow M! The low values in F and T2 could be due to disturbances of these soils by burning and erosion (F) and grazing (T2). For the absolute minimum in T6 of both species-and individual-numbers there is yet no explanation at all.

Altogether Oribatei abundance seems not to be correlated with altitude, but rather with local soil- and vegetation patterns. Also the decrease in species numbers differs from that in Coleoptera. It is by far not as steep and drops from 48 (Z) to 27 (L) only (in Coleoptera from 106 to 8). Summarizing the species from both meadows (M + W) (Table 2), the number becomes the same as in Z (=48). These facts are in accordance with the much larger vertical distribution of the Oribatid species. On the other hand, values from the sites above 2300 m (except T6, see above) have the same size. Treating the "wet" meadow (W) and the "dry" (M) separate, the trendline for species numbers shows a pronounced peak in the *Pinus cembra* soil (Z) and drops steeply to a more even situation in the upper life zones.

Corresponding with these heavy oscillations of data on abundance and species numbers, the diversity also oscillates heavily. All the trend-lines, especially that for the latter ($H(S)$) show a rather uneven course. Maybe aggregations and the small scale mosaic pattern of the environment have such influence, that the amount of sampling is still too small. More data are needed.

Similarity comparisons have been made by the Sørensen Quotient (QS) for Coleoptera and Oribatei (Table 2). The QS for Coleoptera was calculated from pitfall-trapping-results. For both Coleoptera and Oribatei some sites are grouped together, relating them to vegetation-types. In spite of the evidently high correspondence between valley and high alpine meadows, based on the comparison of percentages of high taxa (see above), this correspondence at the species level is only 16 in

TRENDLINES OF CHANGES WITH ALTITUDE: ORIBATEI (O) —, COLEOPTERA (C) - - - ;
 DIVERSITY (Shannon-Index) $[H(S)] = \Delta(C)/\Delta(O)$; SPECIES-NUMBERS (spp.) = $\blacksquare(C)/\square(O)$;
 INDIVIDUAL-NUMBERS (I) $[\bar{x}/s.u.] = \bullet(C)/\circ(O)$ FOR THE INVESTIGATION TIME 1975

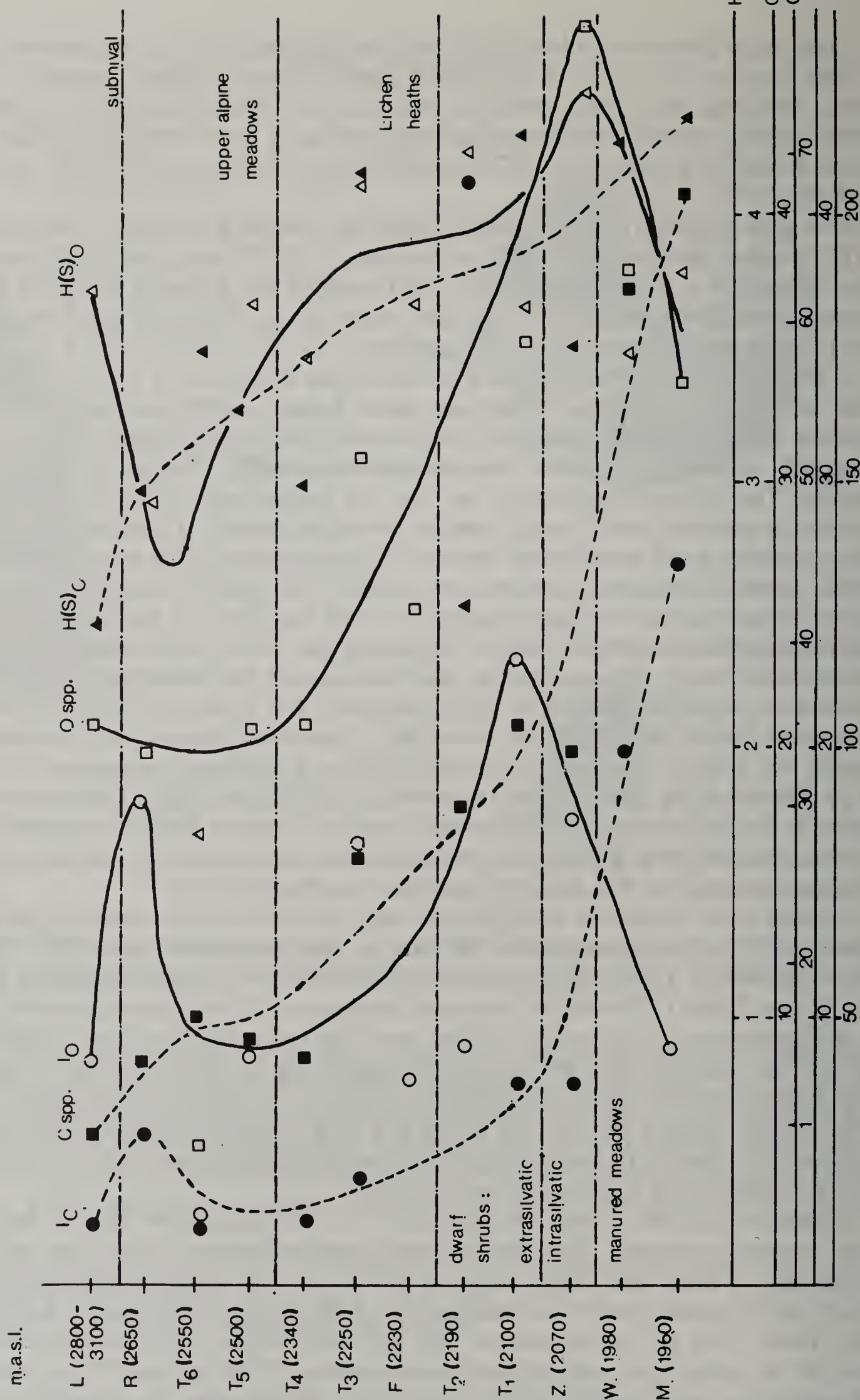


Fig. 3. – Trendlines of changes with altitude for individual- and species-numbers and diversity for Coleoptera and Oribatei, 1975.

Letters M to L indicate investigation sites (F for Oribatei only). The single plotted data show some heavy oscillations. It has been tried to smooth them out by ocularly made trendlines. Diversity is calculated by the Shannon-Index

$$H(S) = - \sum_{r=1}^s (p_r) \cdot (10 \log_2 p_r)$$

whereby s = total number of species at that site, p_r = part of the r^{th} -species on the mean total individuals at the site. If there would be only 1 species, $H = 0$. If all species at the site would have the same abundance, than $H(\text{max}) = 10 \log_2 s$

Coleoptera faunation between M+W/R. It decreases to 4.3 in comparing the still now scanty photo-elector-data 1974 W/R (only these are determined). Only one species was trapped in both sites: the little flower Staphylinid *Anthophagus alpinus*. That QS difference between the pitfall- and photo-elector-data means possibly that these two methods do select different strata. In Oribatei the

Table 2.

SIMILARITY OF FAUNATION SHOWN BY SØRENSEN'S QUOTIENT:

COLEOPTERA		W , M	T ₁ , T ₂	T ₃ , T ₄	R	L
a . b	manured meadows W, M (1960 - 80m) (106 spp.)		39	27	10	3
	dwarf shrubs T ₁ , T ₂ (2100 - 90) (56)	48		28	8	3
	Lichen heaths T ₃ , T ₄ (2230 - 40) (34)	39	62		8	3
	alpine meadow R (2650) (16)	16	22	32		5
	subnival L (2800 - 3100) (8)	5	9	14	42	
		QS				

$$QS = \frac{2c}{a+b} \times 100$$

a = no. of spp. in habitat A

b = no. of spp. in habitat B

c = no. of spp. common to both habitats

ORIBATEI		W , M	T ₁ , T ₂	F , T ₃ , T ₄	R	L
a . b	manured meadows W, M (1960 - 80m) (48 spp.)		28	28	16	18
	dwarf shrubs T ₁ , T ₂ (2100 - 90) (41)	53		34	20	20
	Lichen heaths F, T ₃ , T ₄ (2230 - 40) (43)	62	81		18	19
	alpine meadow R (2650) (25)	44	61	53		19
	subnival L (2800 - 3100) (27)	48	59	54	73	
		QS				

correspondence between M+W and R is even the lowest of all and that of M+W/L still larger. Instead of which, in Coleoptera, the QS for M+W/L has dropped to 5% only, the lowest value of all comparisons made (except the above for photo-elector-data, which possibly are still too scarce). This small but existing correspondence is due to 3 species. Two of them were till now said to be typical high alpine forms (*Oreonebria castanea* Bon. (Carab.), *Dichotrachelus stierlini* Gdlr. (Curcul.)). It was a great surprise to detect them at those low altitudes!

Generally, relations are as is to be expected by former experience: The very regular decrease in numbers of species in beetles corresponds with an altitude-correlated decrease of QS, being likewise regular.

Values for Oribatei are much more uniform. The difference between the largest and the smallest value is 37, in beetles 57.

In both systematic groups the correspondence is highest between the dwarf-shrub sites and the lichen-heaths: Oribatei 81%, Coleoptera 62%. Also here the greater uniformity of the QS for Oribatei can be explained by the wider vertical distribution of the mite species. Oribatei species are distributed more uniformly over the investigation sites.

Now we turn to altitude- and vegetation-related changes in dominance structures at the species-level. These changes in Coleoptera already became evident to some extent at the family level (Fig. 4). In the lower altitudes Staphylinidae predominate clearly, in the alpine meadows Carabidae, and in the subnival site Curculionidae. Dominance structure seems to be most complex in the lichen-heaths and in the high alpine meadows.

Changes in dominance structure at the species level in Coleoptera are shown in Fig. 5. Species are indicated by numbers and symbolized according to that investigation site, where the species in question has the highest dominance. Already by means of the dominance it seems evident that there is a series of beetle communities or clusters detaching one another with increasing altitude. This is especially evident with the lichen-heaths sites. Corresponding with more or less wide vertical distribution of many of these dominant species, these communities are more or less interlocked. We will not go into details of biocoenotics, but if we would take into consideration not only abundances but also vicariations and concordances of less dominant species, the picture would become much clearer. Since those species with a restricted distribution often have a very low density, they will perish when only the dominance structure is considered. Detailed cluster analyses will be made in the future. It should be mentioned that with the reappearance of a closed grass cover in the high-alpine-meadow-belt, species of larger size can again reach high densities, which can especially be said for Carabids (no. 1, 2, 3 of Fig. 5). Thereby *Amara quenseli* Schh. (no. 3) and *Nebria germari* Heer (no. 2) have a restricted vertical distribution and have not been found deeper than in T5 (2500 m), but they also occur in the subnival site L. The third-rank carabid of larger size (*Oreonebria castanea*, no. 1) has been found in all sites down to 1960 m (see above). These three carabids are also known to be very indicative for snow-bed-formations of higher altitudes. Snow beds are not taken into consideration here, since we have just begun to study them.

Changes of dominance structure with altitude for Oribatei-species are shown in Fig. 6. As with Coleoptera, here also a series of different clusters can be recognized by means of the changing dominance, but much less clear as in Coleoptera. Oribatid species in general have, as already said, a much wider vertical distribution, and for more thorough analyses the single samples should better be treated first without relating them with (simplified) environment-parameters. Having compared altitudinal changes, we will now turn to the question of seasonal changes by comparing data from different life-zones, also exemplified by Oribatei, Coleoptera, and the photo-elector-sampling-results, neglecting the seasonal variations of the pitfall-contests on the whole.

Seasonal Variations in Different Life-Zones

Seasonal variation of Oribatei 1974/75 (Fig. 7): Comparison is made between the 2 intensive stations valley meadow (W, 1980 m), and the high alpine meadow (R, 2650 m). Only at the low altitude site was sampling possible over the whole year. At the high alpine site winterover sampling must be stopped rather completely because of the enormous snow-cover depth, danger of avalanches, and the difficult access to the site. Interrupted lines indicate sample series with large variations. Statistical data processing as standard-error calculation e.g. and other is not yet finished for the total Oribatei but for single species only. In 1974 a steep increase in population density can be seen in R, which is especially due to the nymphs. It occurs immediately after the longlasting snowcover has

DOMINANCE-CHANGES WITH ALTITUDE : ORIBATEI, 1975

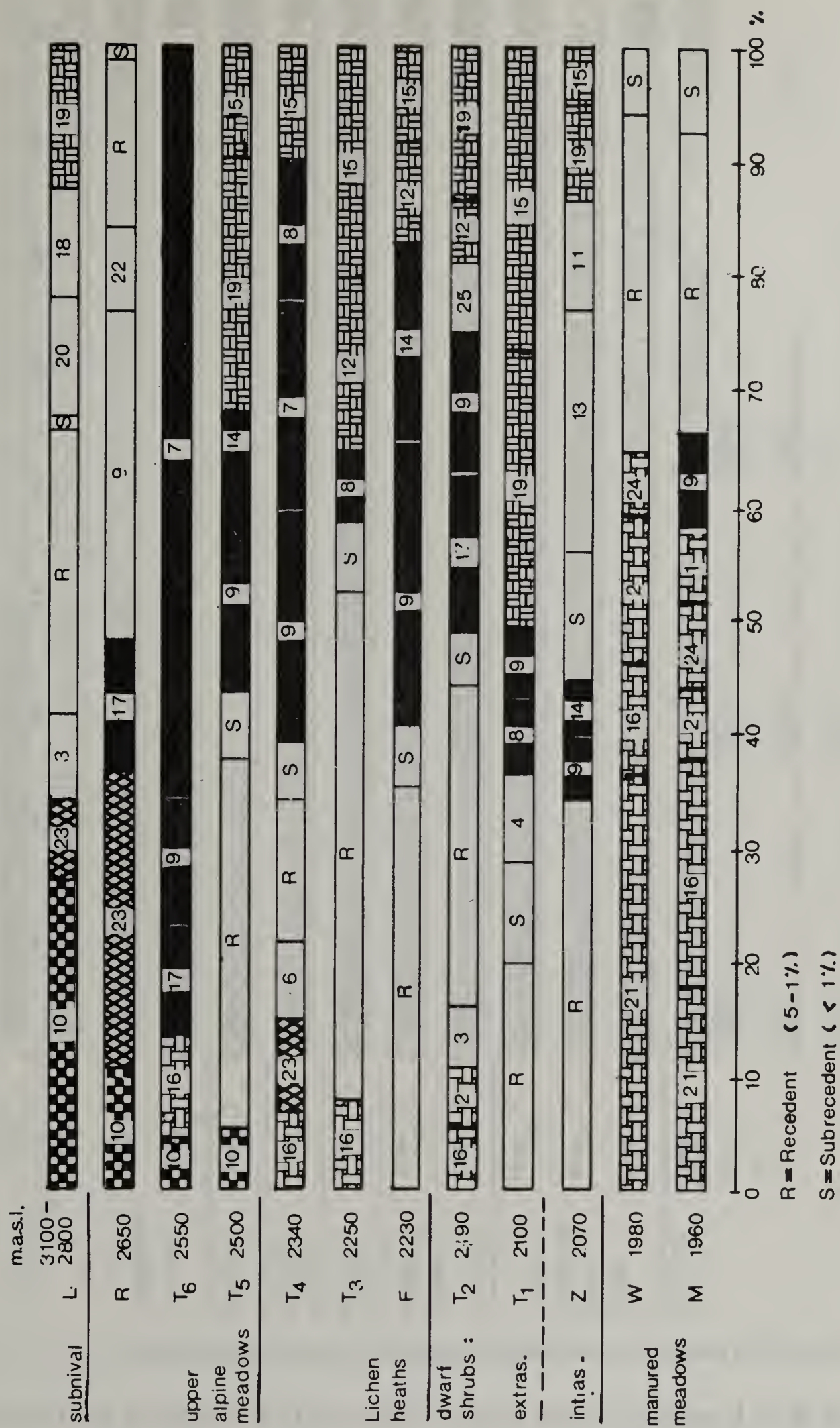


Fig. 4. - Changes with altitude of dominance-structure in Coleoptera-families, 1975.

Letters M to L see Fig. 3.

Total number of families 35, of species 139.

DOMINANCE - CHANGES WITH ALTITUDE : COLEOPTERA SPECIES, 1975

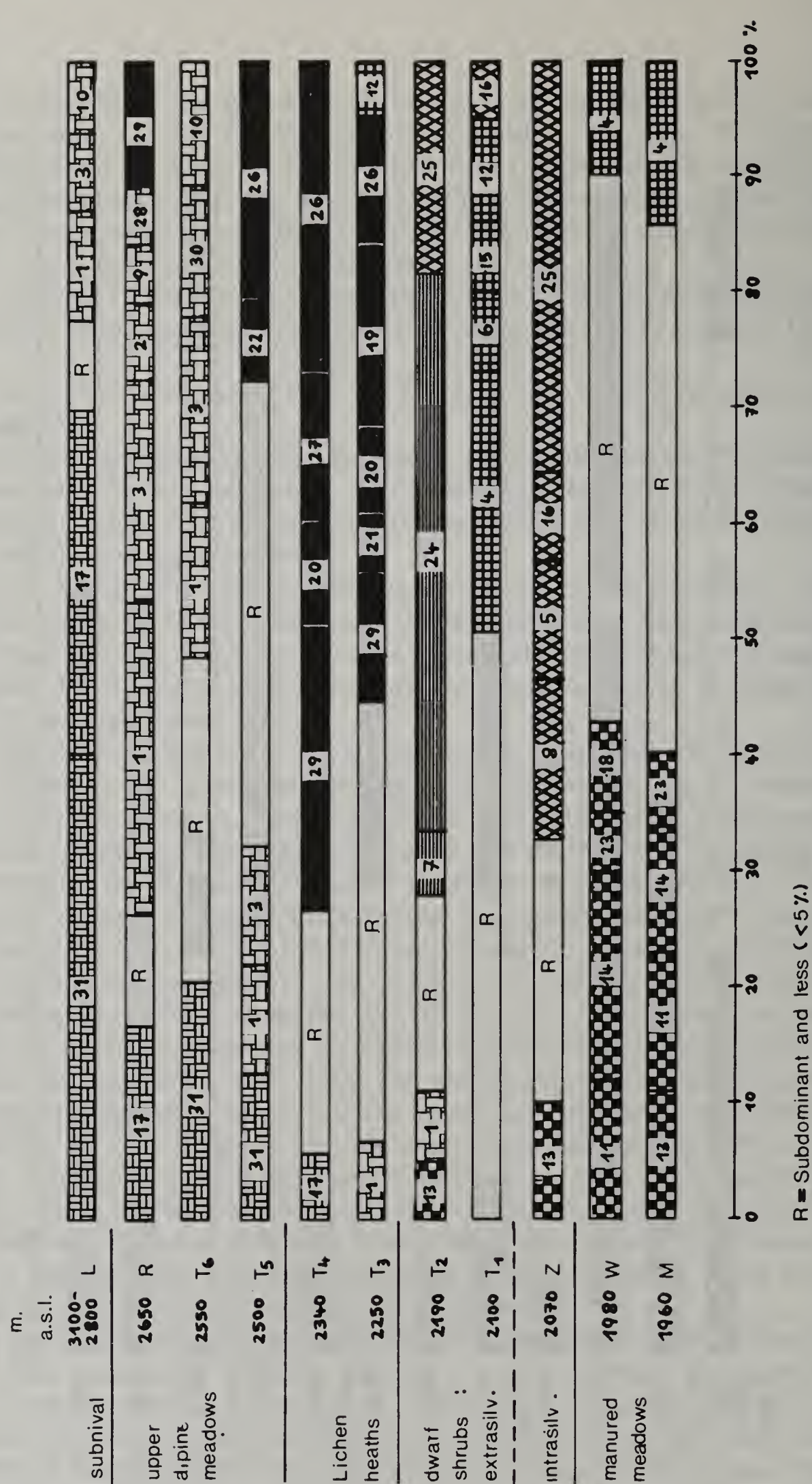


Fig. 5. - Changes with altitude of dominance-structure in Coleoptera-species, 1975.

Letters M to L see Fig. 3. Total number of species 139, of families 35. The numbered dominant species (representing 8 fam.) are:

Carab.: 1. *Oreonebria castanea* Bon., 2. *Nebria germari* Heer, 3. *Amara quenseli* Schh., 4. *Pterostichus jurinei* Panz., 5. *Haptoderus subsinuatus* Dej., 6. *Calathus micropterus* Duft.; Catopidae: 7. *Catops nigricantoides* RH.; Staphyl.: 8. *Omalium ferrugineum* Kr., 9. *O. caesum* Grave., 10. *Coryphium gredleri* Kr., 11. *Philonthus aerosus* Kiesw., 12. *Ocypus brevipennis* Heer, 13. *Quedius punctatellus* (Heer), 14. *Q. dubius* Heer, 15. *Q. ochropterus* Er., 16. *Q. sturanyi* Gglb., 17. *Q. alpestris* Heer, 18. *Q. haberfelneri* Epph., 19. *Mycetoporus mulsanti* Gglb., 20. *M. erichsonanus* Fag., 21. *M. nigrans* Pand., 22. *Bryoporus tirolensis* Jatz., 23. *Tachinus corticinus* (Grav.), 24. *Liogluta nitidiuscula* Sharp., 25. *Atheta leonhardi* Bh.; Canthar.: 26. *Rhagonycha maculicollis* Märk.; Dasyt.: 27. *Dasytes alpigradus* Kiesw.; Byrrh.: 28. *Byrrhus fasciatus* Forst.; Scarab.: 29. *Aphodius mixtus* Villa; Chrysomel.: 30. *Phytodecta nivosus* Suffr.; Curculion.: 31. *Dichotrachelus stierlini* Gdlr.

DOMINANCE - CHANGES WITH ALTITUDE : COLEOPTERA FAMILIES, 1975

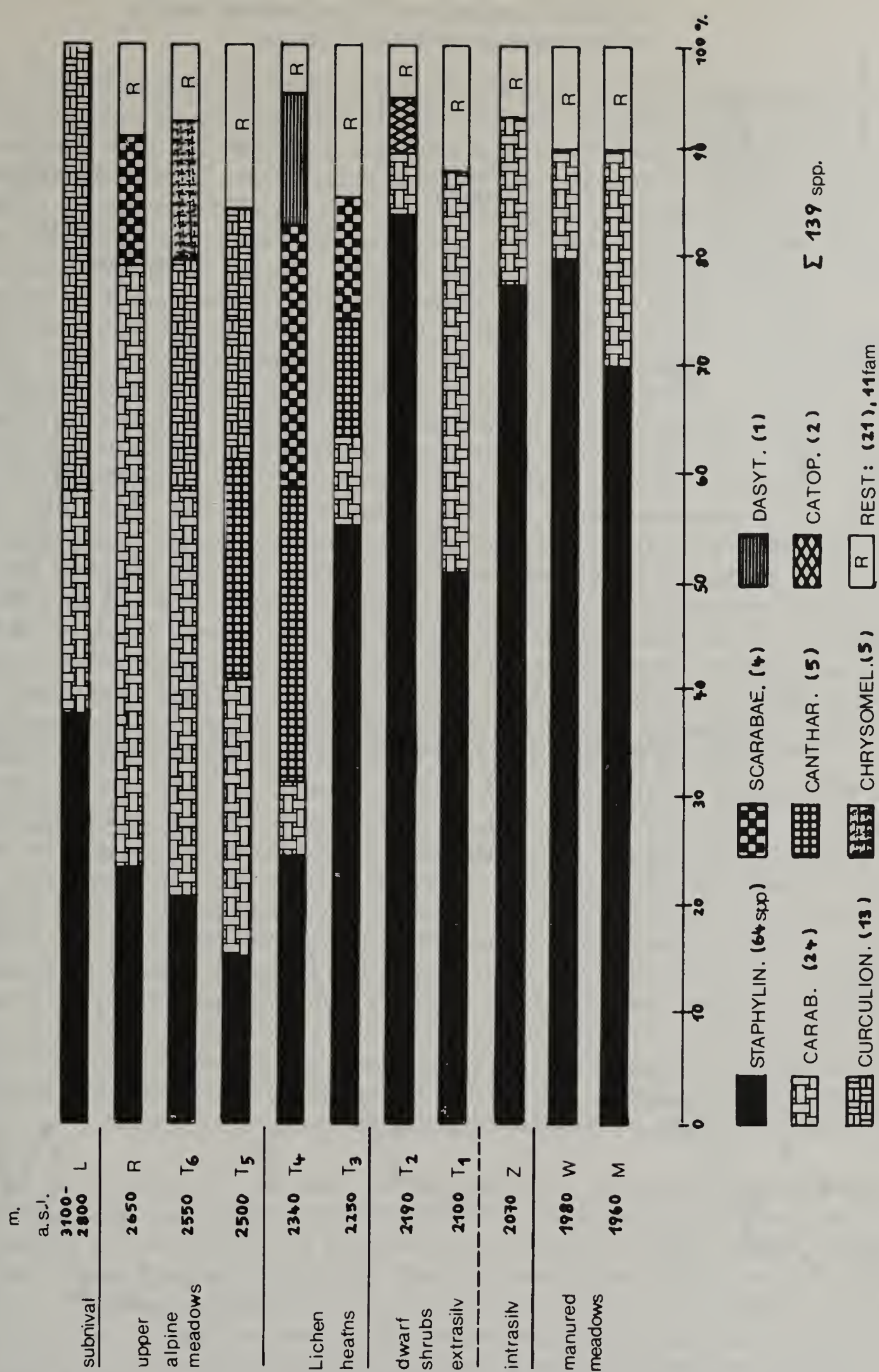


Fig. 6. - Changes with altitude of dominance-structure in Oribatei, 1975.

M to L: see Fig. 3. Total number of species: 81, of families 35. The numbered dominant species (representing 14 families) are:

1. *Brachychthonius laticeps* Strenzke, 2. *Liochthonius sellnicki* (S. Thor), 3. *Trhypochthonius cladonicola* (Willmann), 4. *Hermannia gibba* (C.L. Koch), 5. *Damaeus diversipilis* (Willmann), 6. *Eremaeus oblongus* C.L. Koch, 7. *Carabodes labyrinthicus* (Michael), 8. *C. minusculus* Berlese, 9. *Tectocephus sarekensis* Trägårdh, 10. *T. velatus* (Michael), 11. *Oppia ornata* Oudemans, 12. *O. fallax* Paoli, 13. *Oppiella nova* (Oudemans), 14. *Suctobelbella subtrigona* (Oudemans), 15. *Caleremaeus monilipes* (Michael), 16. *Oribella paolii* Oudemans, 17. *Oribatula tibialis* Nicolet, 18. *Zygoribatula exilis* (Nicolet), 19. *Fuscozetes fuscipes* (L.C. Koch), 20. *Melanozetes meridianus* Sellnick, 21. *Oromurcia sudetica* Willmann, 22. *Trichoribates trimaculatus* (C.L. Koch), 23. *Lepidozetes singularis* Berlese, 24. *Achipteria coleoptrata* (L.), 25. *Anachipteria alpina* (Schweizer).

SEASONAL VARIATION OF TOTAL ORIBATEI 1974/75
IN TWO SITES OF DIFFERENT ALTITUDE

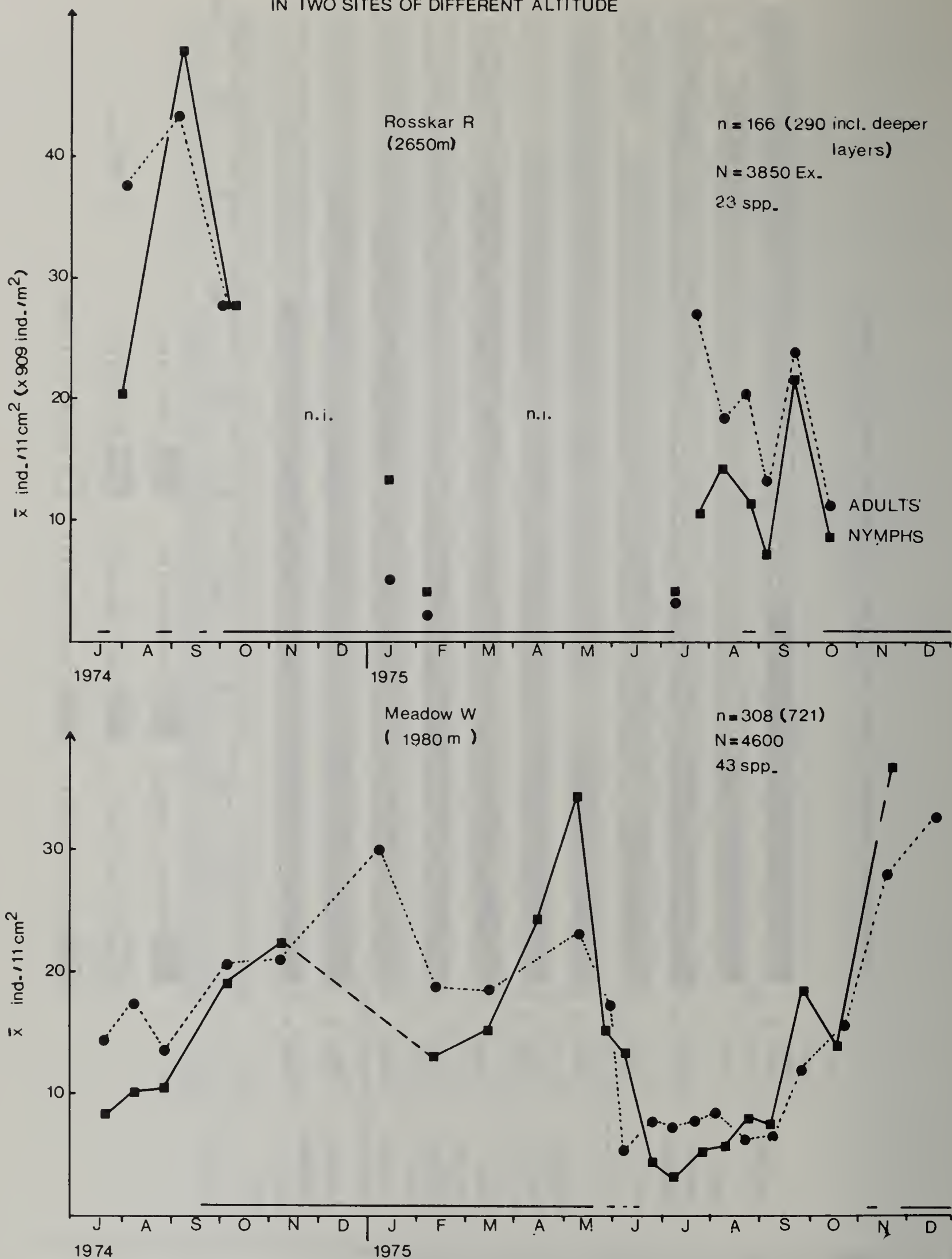


Fig. 7. – Seasonal variations in individual numbers of total Oribatei, 1974/75.

Upper graph: high alpine meadow, Curvuletum, 2650 m (site R)

Lower: Manured wet meadow, 1980 m (site W). (different scales for \bar{x} /s.u.!).

Line above x-axis: Snow-covering period.

n = Number of samples of 11 cm²/0-2 cm depth (in brackets from deeper layers: >2-8 cm, >8 cm; each 2 cm thick).

N = total catch at the site. Extraction was with Tullgren-funnels, width of mesh 1.6 mm, 10 days without heating. Winterover sampling was at wide terms in W, and possible only occasionally in R. Sampling started 1974-7-18 in W and 1974-8-01 in R.

For soil parameters see Table 1.

Drop of data in R Aug./Sept. 75 related with wild weather (see expl. to Fig. 10).

disappeared. Also the next year the same happened, if we take the first separate signed low sampling result immediately after the disappearance of the snowcover as reliable. The depression at the end of August corresponds with bad weather at that time with a new short lasting snow cover of 40 cm. Such depressions can also be seen in other diagrams later. Thus there is an explosive population development in R concentrated in the short vegetation period. Conditions in the valley meadow W seem to be rather opposite: Population development seems to continue under the snow cover, nymphs are found throughout the year, clear cut times of hibernation and cessation of development evidently do not exist, and minimum values are found during June to early September.

Fig. 8 shows that this surprising fact can be related with the population development of one single species, which is by far dominant in that site (*Oromurcia sudetica* Willmann). This species reaches its population peak under the snow cover during January to March. The large standard-errors over this period are due to the lower amount of sampling in winter. Comparisons between subsurface soil temperatures and number of individuals gave a strong correlation between them. Over the two study years the correlation coefficient for the total number of individuals was high ($r = 0.75$, for $n = 21$ and $p < 0.001$) and also for *Oromurcia* ($r = 0.74$). When temperatures fell, abundance of *Oromurcia* did increase. The site was snow covered from October to the end of May with a maximum depth of 2 m. Therefore temperature fluctuations were small in the uppermost soil, still smaller in deeper layers. Even when air-temperatures fell to about -20°C , soil-temperatures were rarely below -3°C , and in winter mostly between -1°C to 0°C (H. Schatz and H. Janetschek, 1976, Unpubl.).

Evidently *Oromurcia sudetica* can use periods of low temperatures for population turnover and is possibly superior in competition during those times. On the other hand it is hardly understandable, given such a temperature resistance, that this species has only been found up to site F (2230 m). Experimental work on the temperature ecology of this species has still to be done.

Seasonal variations of other Oribatids in W can be quite different from that of *Oromurcia*. *Oribella paolii* Oudemans e.g. (9% dominance in the mean of 1974/75) shows an increase during summer (but without significant correlation with temperature (Schatz and Janetschek 1.c.)). For comparison with the alpine meadow (R) *Lepidozetes singularis* Berlese is plotted in Fig. 8. In the mean of 1974/75 it is the second dominant species with 22% behind *Tectocephus sarekensis* Trägårdh (30%). The population development of this species coincides with that of the total Oribatei.

Discussions on seasonal variations in Coleoptera will also be restricted to a comparison of W with R, based on pitfall-trapping-results. Therefore we handle only seasonal changing activity-densities (Fig. 9). Because of the snow cover, first setting of the traps in 1974 in R (1.8.) was later than in W (18.7.), therefore also the first emptying. By the same reasons as with Oribatei, trapping in R was impossible in winter. In 1974 we cannot say if data of first emptyings indicate a peak or lie on a decline. But in 1975 there is a very steep rise to a high peak end of July in W and a little bit delayed in R.

After this peak the decline of activity is interrupted by the mentioned bad weather period. After that a new, smaller peak occurred in both sites. We know nothing about winter activity in R. In W winterly activity still continues, and becomes very small only in March to May. Responsible for that is (besides other species the staphylinid *Quedius haberfelneri* Epph. (last line in Fig. 9). As always, only adult beetles are considered, since too few larvae have been caught and these are not thoroughly determined. For comparisons on the species level some of the most dominant ones have been used. Statistical data processing has not yet been done. Due to the low densities even of the highly dominant species it is not so easy to get sound results. Nevertheless the temperature fall with snow cover in R is clearly visible in all plotted species, also in W. Very striking are the large differences in activity densities in the two subsequent years, *Amara quenseli* being highly dominant in 1974 and *Oreonebria castanea* in 1975. Also *Philonthus aerosus* Kiesw. (in W) shows this fact very well.

We will not enter in discussions of life-cycle-problems, but an explanation could be given by the assumption, that the species population is composed by several non-synchronized strains with shifted life-cycles of several years duration. Hence adults could appear in batches of different quantity in subsequent years. Seasonal variations as shown by photo-elector-sampling-results (Fig. 10) give the same evident relation with length of snow-free period (like vegetation period). With a certain delay after the disappearance of the snow a steep rise can be seen, followed by a lower decrease later on, interrupted by the already mentioned temperature fall and building up of a short lasting snow cover at the end of August, followed by a new increase in hatching activity at the end of the season (Fig.

SEASONAL DISTRIBUTION OF TWO DOMINANT
ORIBATEI, 1974/75.
MEAN \pm 2 SE (SE = $\frac{1}{\sqrt{n}}$)
SNOW COVERING (SC)

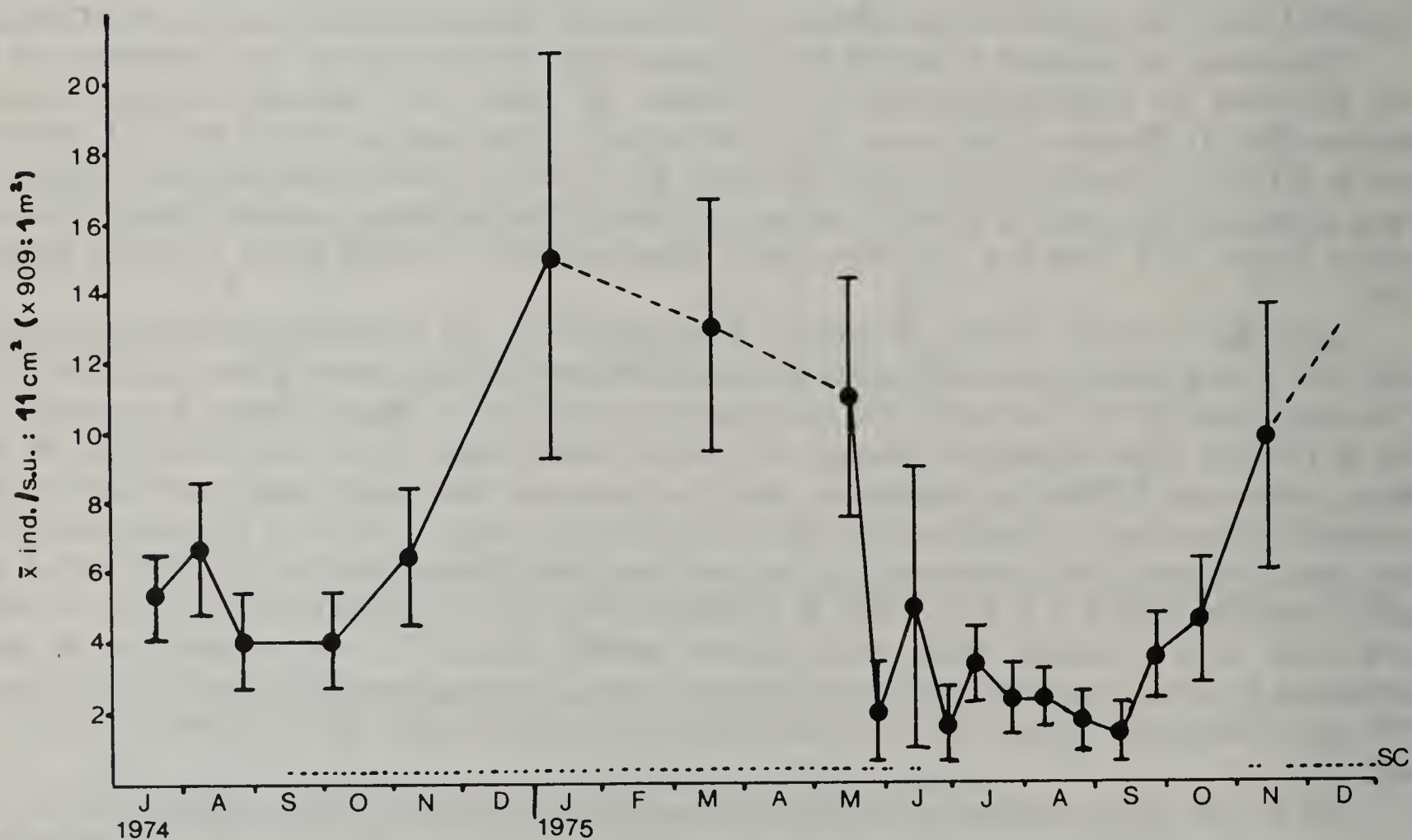
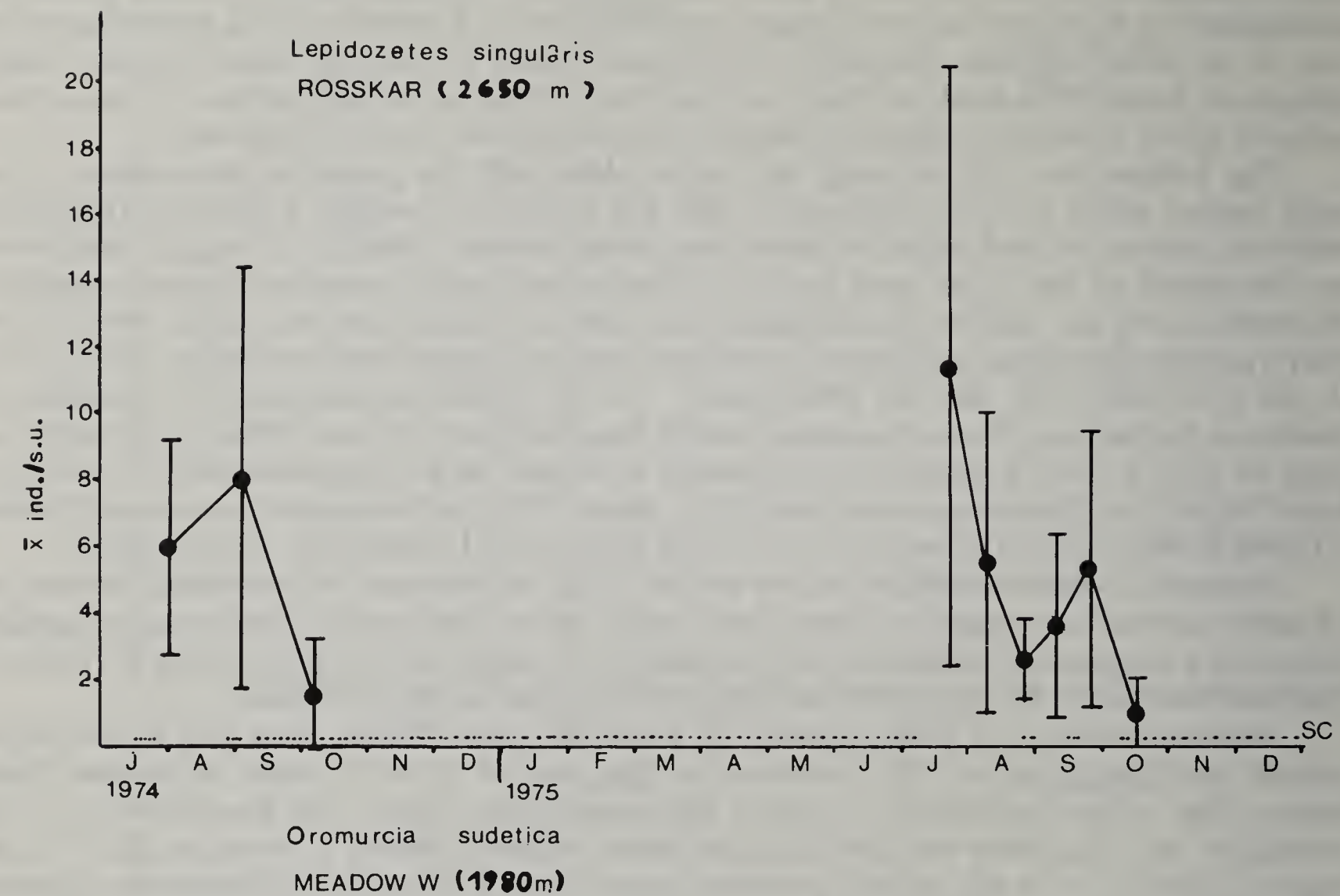


Fig. 8. — Seasonal variation in individual numbers of two dominant Oribatei species 1974/75.

Upper graph: high alpine meadow (Curvuletum), 2650 m (site R).

Lower: manured wet meadow, 1980 m (site W). Plotted are the means \pm doubled standard errors.

Hatched line above x-axis: Snow-covering period (SC). For further explanations see Fig. 7, for dominance structure Fig. 6, no. 21, 23. Drop of data in R Aug./Sept. 75, see expl. to Fig. 7.

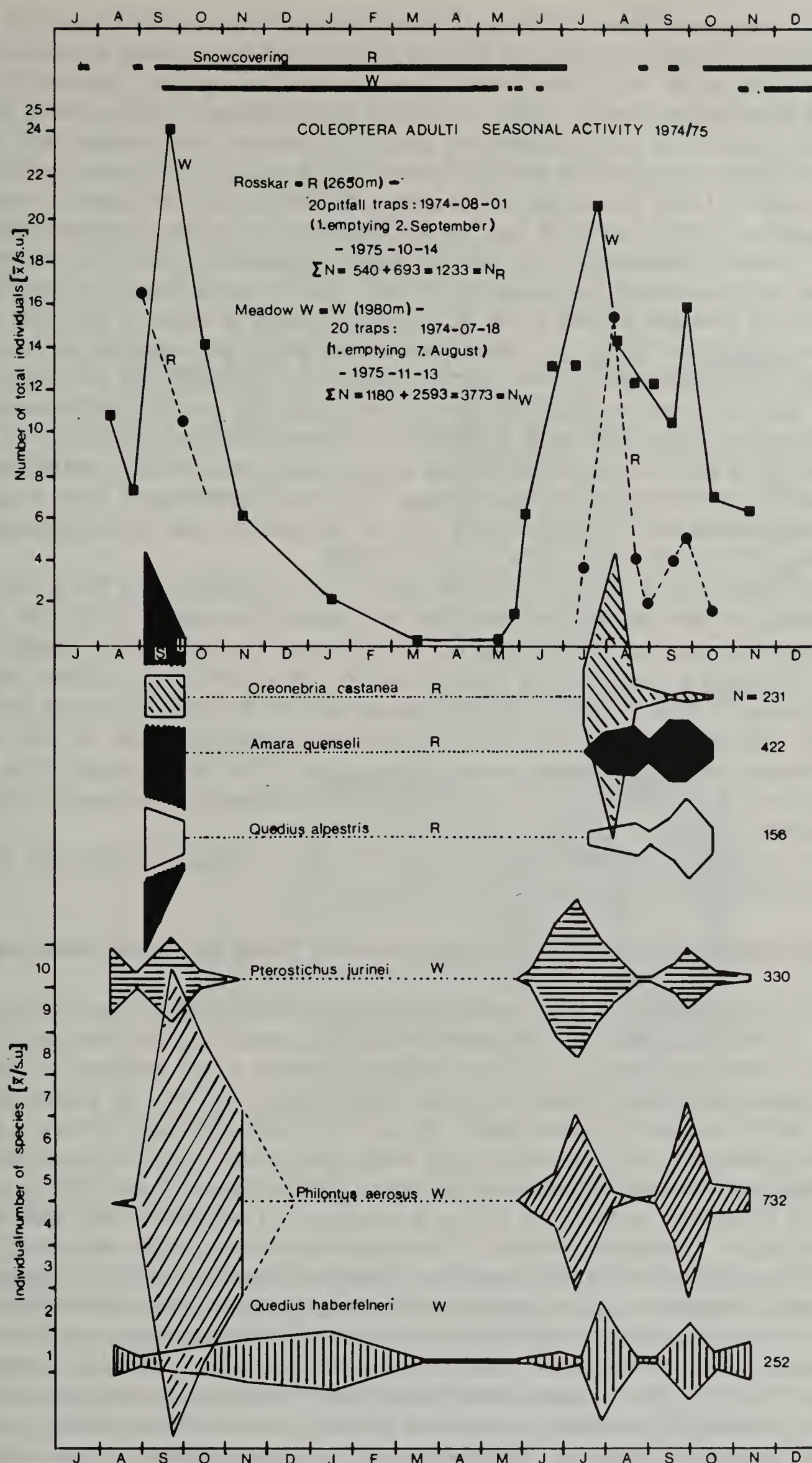


Fig. 9. – Seasonal variation in Coleoptera 1974/75 in a high alpine meadow (*Curvuletum*, R, 2650m) and a manured wet meadow (W, 1980m). (Pitfall-trapping results. Adults only plotted).

Upper: Changes of total activity density.

Lower: Changes of some dominant species. They correspond from above to below with no. 1,3,17,4,11,18 in Fig. 5. Drop of data in Aug./Sept.75 due to wild weather (see expl. to Fig. 10).

10a). In the valley meadows (M and W; M not plotted) this production is, after the first steep rise, more evenly distributed over the most part of the vegetation period July to early September.

Some 1976-data for the valley meadows are already available (Fig. 10a). Apparently due to the different weather situation with heavy dryness in the first half of this year, the first steep rise (only W plotted) is shifted to an earlier time, followed by a very pronounced steep decline. With interest we wait for the results from the rest of this year: Will a new peak occur, or is the greater part of hatching completed by the end of June? Thus it can be concluded, that the total of the events, covered by that method (mxp. hatching activity of flying insects) is strongly influenced by exogenous parameters. If we differentiate seasonal variations on the level of higher systematic groups (for the species-level determinations are still too scarce), a sequence of different aspects can be found. A comparison of the changes in percentage between W and R for all dominant groups is made in Fig. 10b and c. The respective annual mean % are given too. Data from pitfalls would give a similar picture. A further differentiation to the family-level in the Diptera, which are most of the time first dominant (considering the seasonal peaks of the totality only (see Table 3)), gives us the following series of aspects: in W: Lycoriidae – Phoridae. In R: Lycoriidae – Hymenoptera (of small size!) – (Tipulidae). The Tipulid-aspect in R near the end of the season is not yet safe, since the size of that catch is very small. It needs to be verified by further investigations. The total Diptera-fauna in W is composed of 24 families (9 Nematocera = N, 15 Brachycera = B) (at the present state of data processing). This relation changes in 1975: 1.: 8N, 9B; 2.: 5N, 11B; 3.: 4N, 8B.

Relations in R with a total of 15 families (6N, 9B) are: 1.: 4N, 5B; 2.: 3N, 7B; 3.: 4N, 2B.

It is worthwhile to give also the available data on Diptera from spring 1976 in W. Traps have been set there immediately after the progress of melting made the installations possible. The first emptying (4.6.76) showed a dominance of Diptera, with $N : B = 1.44$ (59:41). Taken the Diptera = 100, Lycoriidae came to 45% (= 75% of N). Chironomidae 14% (= 14% N). At the 2nd emptying (11.6.76) the $N : B$ relation was 32 (97:3), Lycoriidae having increased to 96% of the N, Chironomidae dropped to 3.8% (the rest were Cecidomyiidae). The 3rd emptying (18.6.76) gave a high total peak with the same $N : B = 97:3$ (32). Lycoriidae still increased to 95% of N, Chironomidae further dropped to 2% N.

The picture resembles therefore that of the first peak in 1975, also with the Lycorriidae-aspect, but on the whole earlier and about twice as big as in 1975.

Considerations on Productivity Differences Between Valley and Alpine Meadows

We desisted from weighing of whole assemblages (total catches), which could give a quick first rough estimate of total biomasses in comparison with other totals. In the long run it would be necessary anyway when attempting to work on ecosystem-analysis to get the data for single species and their stages respectively, and to build up biomass-data slowly that way. At present we have too few weight-data for the numerous species, which spread over a large size-range. Diptera e.g. from our investigations area, basing on our freshweight data, range from about 57 μ g (Chironomidae) up to 18 mg (larger Muscidae), weights in Coleoptera range still much larger (see e.g. Lang, 1975).

The oribatid *Oromurcia sudetica* (in W) has a calculated (!) weight of 65 μ g. This value lies in the middle of the order of calculated weights of the species assemblage on the whole in W. Therefore it could be used for an approximate transformation of individual numbers to Oribatid-biomasses in W, but without having comparisons yet. At present we must be content to deal with individual numbers. At the present state it doesn't seem worthwhile to touch production problems. But first attempts to get some estimates, based on individual numbers only, will be made. The soil-sampling-data on Oribatei ($\bar{x}/11\text{cm}^2$) and the photo-elector-data ($\bar{x}/d/0.25\text{m}^2$), both allow comparisons of estimates of production in W and R.(a) Production comparisons by means of total Oribatei. Data processing was

Production comparisons by means of total Oribatei. Data processing was done as follows: The difference in numbers of nymphs plus adults between the sampling terms considered, taken from Fig. 7, gives the increase of individuals in the given time. From the number of days between the respective terms considered, one day was subtracted, under the pragmatic simplification, that sampling was about midday. In order to make different time-periods comparable, the increase per number of days was reduced to increase/day. Total Oribatei in R shows a pronounced rise in 1974 from the 1. to the 2. sampling terms (R1), and a smaller one in 1975 from the 7.8. (R2) (after return of good weather after the bad weather break). Comparing these rises with a series of periods of rises in W, the following relations turn out:

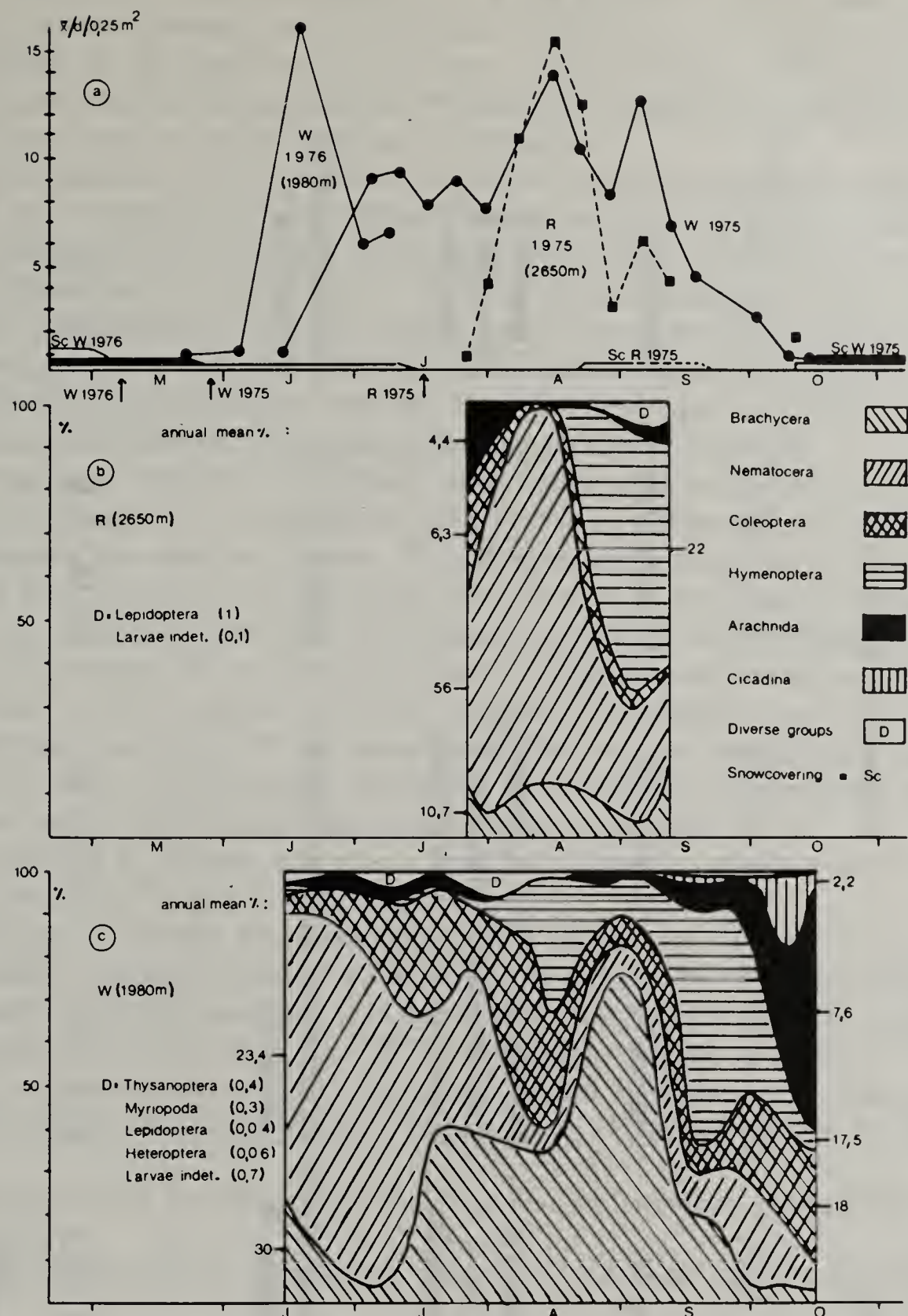


Fig. 10. – Seasonal variations in results of emergence-trapping by photo-electors in a valley-meadow (W) and in a high alpine meadow (R).

a) Changes of mean individual output per day and 0.25m². For the graphical comparison between R and W only the data at the end of each operating period are plotted. To convert them into totals of periods each, column-series must be drawn. (See Fig. 11). Spring data 1976 for W are also plotted, everything else in a) concerns with the year 1975 as it is in b) and c). Sc = Snow covering (indicated along x-axis). Arrows below x-axis indicate first setting.

b) Seasonal changes of dominant groups in a high alpine meadow (*Curvuletum*, 2650 m).

c) The same in a manured wet meadow (1980 m). Lateral to b) and c) the annual mean percentages are given.

Traps (see also Fig. 2) operated as follows:

In W 141 days (setting 28. Aug., 13 days after snowcover began to disappear, till 15. Oct., emptying till 4. July 3-weekly, thereafter weekly). In R 59 d (setting 15. July, immediately after snowcover-retriate made it possible, till 12. Sept., emptying weekly. Interruption from 12.-23. Sept. due to foregoing wild weather (23./24. Aug.) with snowcovering of 40 cm and a drop of temporary snow-line to 2200 m for about one week. New working of control traps 23. Sept. -9. Oct. after return of better conditions).

Table 3—Seasonal aspect-changes at peaks of hatching activities, 1975
(by time-sorted photo-elector samplings; % of each total catch).

Site:	Meadow W, 1980m			Curvuletum R, 2650m		
Investigation period	4.7. — 11.7.	7.8. — 16.8.	29.8. — 5.9.	7.8 — 15.8.	28.8. — 5.9.	23.9. — 9.10. ⁺⁺⁺⁾
Dominant groups	Diptera 76	Diptera 36	Diptera 70	Diptera 98	<i>Hymenoptera</i> 56	Diptera 23
dom. family of that next —//—	<i>Lycoriidae</i> 38 Psilidae 14 Chironomidae 5	<i>Phoridae</i> 16 Muscidae 4 Chironomidae 5	<i>Phoridae</i> 60 Chironomidae 3 Lycoriidae 3	<i>Lycoriidae</i> 87 Muscidae 3 ⁺) Chir./Milich.	n.i. n.i.	Tipulidae 9 Muscidae 6 Lycoridae 5
Next dominant groups	Coleoptera 18 Arachinda 4	Hymenoptera 33 Coleoptera 29	Hymenoptera 22 Coleoptera 5	Coleoptera 2	Diptera 37 ⁺⁺⁾	Hymenoptera 22 Coleoptera 6
Relation						
Nemato-cera/						
Brachy-cera (N:B)	67:33 = 2	14:86 = 0.2	9:91 = 0.1	92:8 = 12	72:2B = 2.B	7:3 = 2

+) *Muscidae* next period: >8%. Annual mean 6%

++) *Lycoriidae* 24, *Chironomidae* 2, *Tipulidae* 1

+++) Last period, after 12 days investigation-break by bad weather and snowcover of 40 cm depth.

In 1974, comparing R1 with these periods in W: 1.-2. term/3.-5./1.-5., the increase/day in R1 is 4/4.4/6 times larger than in W. In 1975, comparing R2 with the periods in W: 2.-5./3.-5./9.-14./9.-16./13.-14., the increase/day in R2 is 2.9/4/5.7/3.8/1.7 times larger than in W. The comparatively largest increase in W with the R/W-relation of 1.7 was during the period 3.9.-22.9.1975 actually at the same time as the rise in R2 (5.9.-23.9.1975). In the mean of these relations, it would turn out, that during periods of population growth the high alpine *Curvuletum* (R) is superior over the manured wet valley meadow by 4 times.

The conclusion could be, that the shorter vegetation period in the high-alpine site (2650 m) is well compensated by a population development, which can be 2 to 6 times quicker than in the compared valley meadow (1980 m) (which of course does not seem to be the best site for Oribatids!). The high-alpine Oribatid populations therefore seem to be well adapted to their comparably harsh environment, being "opportunists", which can make a good use of periods of good conditions.(b)

The emergence trapping with the photo-elector-method allows an estimate of the minimum net production as output of individuals over the time between each emptying. Naturally certain shortcomings of the method due to its selecting-operating cannot be excluded.

The trap is especially efficient for positively phototactic holometabolous flying insects. But the contents of their pitfall-traps are included in the data. However, comparisons of results should be real anyway. Data processing was done as follows: With the pragmatic simplification, that first setting of the traps as well as the control of the collecting boxes have been done about midday as well as the final removing of the traps, also here from the number of days of each catching period one day has been subtracted. This number of days multiplied with the mean production on individuals per day and elector (surface 0.25m^2) gives the mean minimum production over that period without considering the unknown mortality. We can summarize them up over sampling periods of any size we choose, which gives us the mean individual production over that time per $\frac{1}{4}\text{m}^2$ (see also Fig. 11). For comparisons we calculated the following values (in terms of $\bar{x} \text{ ind./d}/0.25\text{m}^2$):

1. Total production in W over the whole sampling time (the whole season = 140 days from 28.5.-15.10.1975) per $0.25\text{m}^2 = 964.36$ in 140 days.

2. The production in W over the same time as in R till the interruption of the operating of the traps by the snow-falls (= period from 15.7.-12.9.1975 = 59 days) = 599.19 in 59 days.

3. In R the value for the above time, that means from the beginning of the operating to the bad weather with snowcover of 40 cm (15.7.-12.9.1975 = 59 days) = 390.01 in 59 days.

4. The whole operating time in R, including the period after the break, whereby the value for these 12 days interruption was intrapolated (therefore from 15.7.-9.10.1975 = 86 days) = 439.91 in 86 days.

5. The single value in R for the last period after the bad weather time (23.9.-9.10.1975 = 16 days) = 22.54 in 16 days.

6. The parallel value in W (14.-16.period, reduced to the same number of days) = 43.43 in 16 days.

7. Last period in W (10.10.-15.10.1975 = 5 days) = 2.5 in 5 days.

8. Last period in R (23.9.-9.10. = 16 days, reduced to 5 days) = 6.95 in 5 days.

Therefrom the following relations turn out:

1. In comparing the whole operating times like seasons (values 1:4 = 2.2) the output of the valley meadow W (1980 m) is 2.2 times larger than that in the high alpine site R (2650 m) (comparing the respective data from Fig. 2, that value would be 2.4).

2. In comparison of the operating times from the beginning to the bad weather inbreak (values 2:3 = 1.536), the output of W is 1.5 times larger than in R.

3. In comparison of the last single period in R after the new setting of the traps after the bad weather period with an identical time in W (values 6:5 = 1.95), the output in W is about 2 times larger than in R.

4. In comparison of the last period in W with the last period in R (reduced to the same number of days as in W) (values 8:7 = 2.78), the output at the end of the season is in R about 2.8 times larger than in W at that time.

Taking the mean of the comparisons 1-3(=1.89), the mean output in W is about 1.9 times larger than in R. But this relation changes during the season. This can be seen by differentiating more: If we compare the resp. $\bar{x}/\text{d}/0.25\text{m}^2$ (Fig. 11) for these operating periods which are more or less simultaneously in both sites, we get the following values:

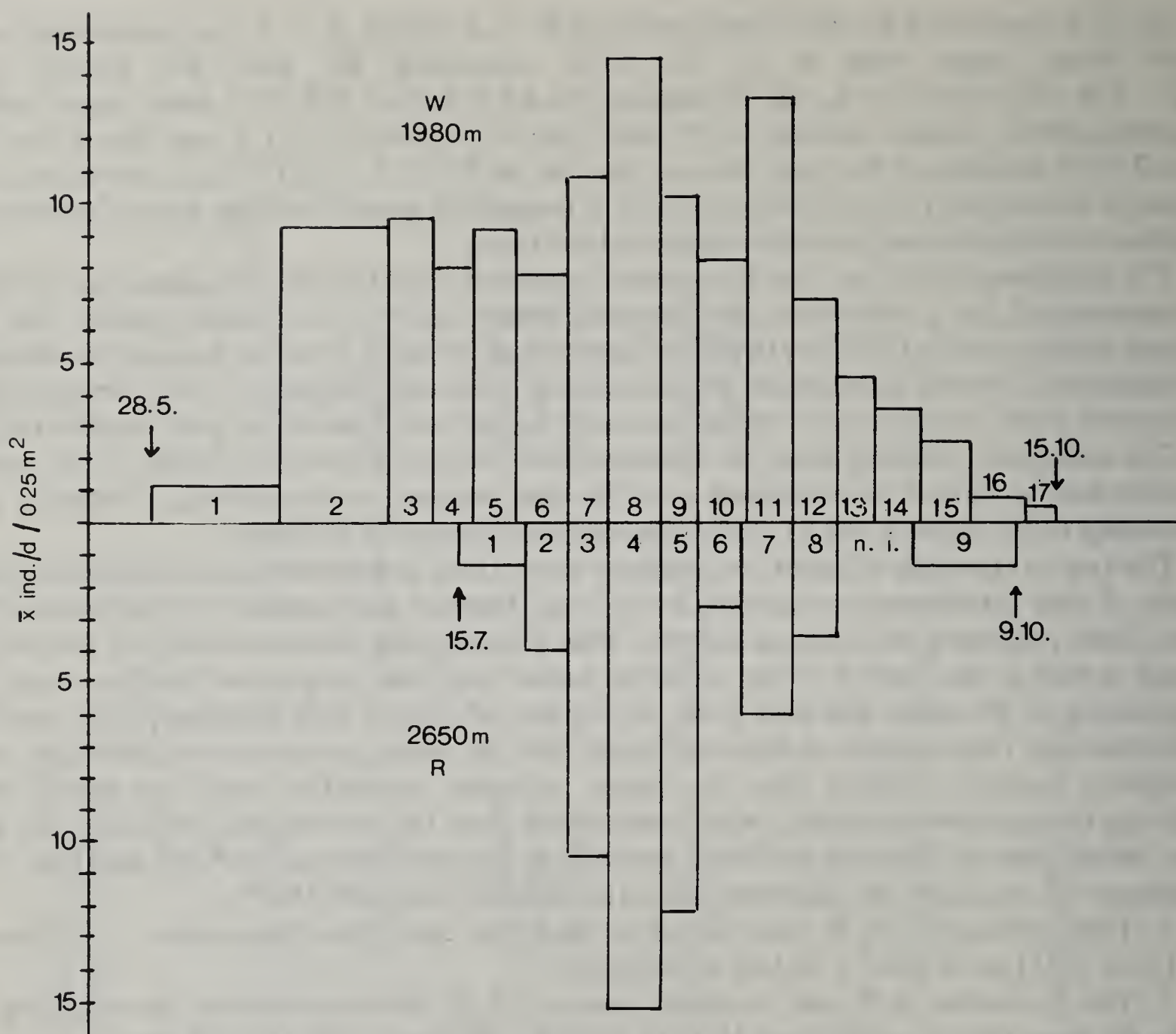


Fig. 11. – Changes in “emergence-trap-production” in a valley meadow (W) and in a high alpine meadow (R) in 1975. Further explanation see Fig. 2 and 10.

- 1: the 1. emptying term in R (period 15.-25.7.) with 5. in W (17.-24.), W:R=7.
- 2: the 4. in R (7.8.-15.8.) with 8. in W (7.8.-16.8.), R:W \approx W:R \approx 1.
- 3: the 7. in R (28.8.-5.9.) with 11. in W (29.8.-5.9.), W:R = 2.2.
- 4: the 9. in R (23.9.-10.10., the last, separate, term) with 15. in W (25.9.-2.10.), W:R = 1.9.
- 5: the 9. in R (s.a.) with 16. in W(2.-10.10.), R:W = 1.5.
- 6: the last in R (9.,s.a.) with the last in W (17.,10.-15.10.), R:W = 2.78.

Summarizing the above data, it can be said: 1: When season in R starts, then in W production is already high, and 7 times larger than in R at the same time. 2: At the peak activity in the season under good conditions (value 2) both sites are equal in (measured!) production ($\bar{x}/d/0.25m^2=14(w)$ and 15(R)). 3: Recovery after the wild weather (between 5. and 6. term in R) was in R lower than in W, which was superior by 2.2. 4: Taking the mean of both peak values, W would still be superior over R by about 1.5. 6: Approaching to the end of season, production in the high alpine site is still going on a little bit (and of the same order as at the beginning (1: 1,32/d,9:1,39/d), whereas that in the valley meadow has already smoothed out (17:0,5/d).

We presented some selected results of our teamwork based on pitfalls, photo-electors, and soil-samples of small size. Results from other methods have been neglected here. Field work with large sized soil-samples, extracted by Tullgren-funnels, and time-sorted Malaise-trappings for diel activity-changes of flying insects, as well as culturing of certain species in the laboratory for bionomic studies are running and the other work will be continued. Now we have also a “light-weight” motorized suction-trap at our disposal, which can be used at the high mountain sites with not too many difficulties, and we hope to improve by that method our quantitative estimates. Progress, however, will not only depend on our scientific passion, but on the extent of further supports too, which we hope very much to get.

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Section 3: Physiology and Biochemistry,

Section 5: Ecology, and

Section 8: Biological Control.

Physiology and Biochemistry of Insect/Host Interactions

Organizer: Dorothy Feir (USA)

Convener and Moderator: L.M. Schoonhoven (Netherlands)

The Role of Chemical Factors in Insect/Plant Relationships

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It is estimated that about one-half of all known species of insects are more or less dependent on plant hosts. Although polyphagy is generally viewed as the more primitive stage in the evolution of insect/plant interactions (Dethier 1954), it seems that presently oligophagy is the rule among phytophagous insects. Thus according to Eastop (1972), in England, 53 percent of the Aleyrodidae, 54 percent of the phytophagous Thysanoptera, 95 percent of the Psyllidae and 97 percent of the Aphididae are specific to a single plant genus. There is evidence suggesting that some highly polyphagous species are in fact conglomerates of more or less host specific biological races. These, quite often, extremely intricate insect/host plant associations involve sensorial, physiological and ecological processes mediated by many environmental factors. There is little doubt, however, that plant allelochemicals are the key factor in the establishment of these associations.

Effect of Plant Chemicals on Insects

Insects live in an environment permeated with chemicals of all sorts. Those of plant origin include chemicals that are released into the air or soil and affect insects before or just when contact is made. Others are compartmentalized within the plant tissues and act upon the insect after they are released following destruction of the tissue. These factors elicit behavioral and physiological reactions, and affect also ecological processes.

Behavioral Effects

Some of the most important effects of plant chemicals on insect behavior are: (a) host-plant selection; (b) aggregation; (c) mating, as a consequence of the possible effect of the food eaten on pheromone synthesis (Hendry 1976).

Physiological Effects

Plant chemicals influence the physiology of phytophagous insects in various ways, some of the most obvious being: (a) nutritional effects on growth and development (Beck and Reese 1976); (b) antinutritional effects through the action of antibiotics, enzyme inhibitors, etc. (Ryan 1973, Ryan and Green 1974, Chapman 1974); (c) hormonal effects through the action of juvenile hormone mimics (Slama 1969); (d) polymorphism and generation alternation in aphids (Mittler and Sutherland 1969), and possibly alternation of phases in grasshoppers (White 1976).

Ecological Effects

Manifestations of the effect of plant chemicals in ecological processes are observed at both autoecological and synecological levels: (a) single species population fluctuations may be a direct result of fluctuating levels of a key nutrient (nitrogen for instance) in the food (White 1976); (b) effect on parasitoids of the food eaten by their hosts (Vinson 1976); (c) effect on predation of food eaten by

the prey, as for example insects feeding on milkweeds (*Asclepiadaceae*) being protected against predators due to the concentration of the plants' cardiac glucosides (Price 1975); (d) production of protective coloration through the concentration of plant pigments such as carotenoids in the animal's body (Rothschild 1975).

Insect/plant interactions can be fully understood only when approached as a holistic phenomenon in community ecology. Competition and predation, evidently play a major role in the final realization of an insect's feeding niche. However, host-plant selection processes are the foundation upon which all other factors seem to rest. It is therefore these processes that I chose to discuss in this paper. The strictly metabolic and nutritional aspects of this interaction were recently reviewed by Beck and Reese (1976).

The Chemical Basis of Host Plant Selection

The uniqueness of secondary plant metabolites, some occurring in a single plant species, others restricted to closely related taxa, offered a logical foundation for the interpretation of host selection processes (Fraenkel 1969). In fact the role of some of these compounds in plant defense mechanisms against herbivores could also be a satisfactory explanation for the very existence of these compounds. The idea of coevolution of animals and plants largely rests on the peculiarities of the distribution of plant natural products, on the specific responses of animals to particular compounds, and on the observation that closely related events usually feed on closely related plants (Ehrlich and Raven 1964).

During the 1950's and 1960's researchers of insect host-plant selection diverged somewhat in the emphasis placed on the relative role played by substances of the primary and secondary plant metabolism in host-selection processes. Figure 1 outlines the biosynthetic relationship among these two classes of substances. The main ideas developed during that period were amply debated and summarized in review articles by Thorsteinson (1960); Beck (1965, 1974); Fraenkel (1969); and Schoonhoven (1972). The argument in favor of the key role of secondary plant products in host/plant selection was based on two main assumptions: firstly, that since plant physiologists provided few, if any, explanations for the existence of most plant natural products, and since these compounds were limited to distribution to a few plant species, genera or families, they could not be essential to basic plant metabolism; consequently the function of natural products should be sought at the plant/herbivore interface. Secondly, that most green plants contained in more or less

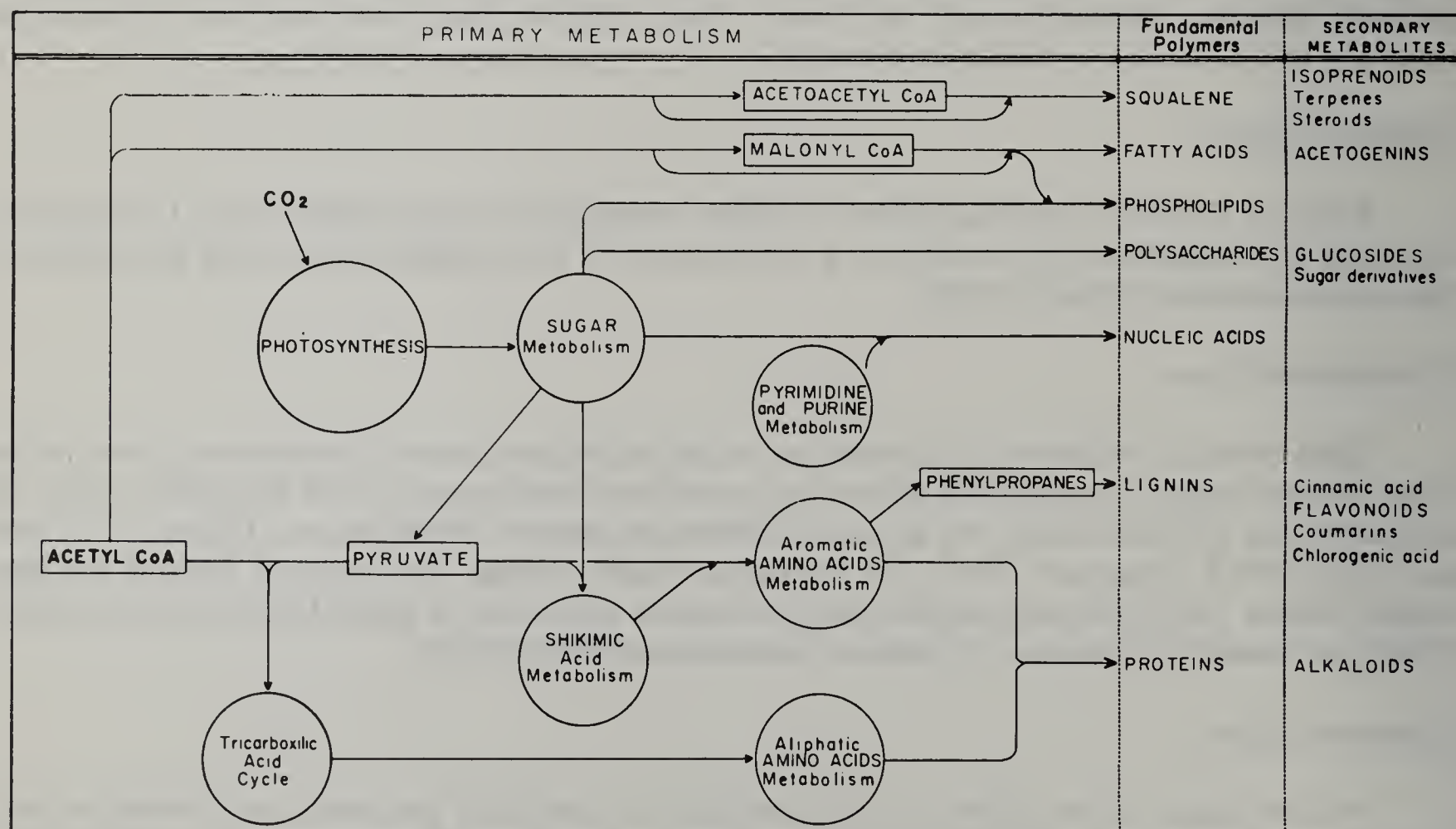


Fig. 1. —Abbreviated scheme indicating main relationships between compounds of plants primary metabolism, their polymers and secondary metabolites.

appropriate amounts the 20 or 40 nutrients that are required by most insects for normal growth and development (Fraenkel 1969).

Although the allelopathic role of plants' natural products in plant/plant, plant/disease, and plant/herbivore interactions is incontestable today the assertiveness of the above assumptions have been greatly toned down. Plant physiologists are finding increasingly important roles in basic metabolism for several secondary plant compounds. Geissman and Crout (1969) pointed out that as recently as 1950 shikimic acid was recorded as an obscure compound that occurred only in the Asiatic plant *Illicium religiosum*; shikimic acid is presently known to be an almost universally distributed compound that plays a fundamental role in the metabolism of aromatic amino-acids. It is apparent also that many of these secondary metabolites are in a state of dynamic equilibrium in plants and they are mobilized into the primary metabolism serving as storage chemicals or as regulators of biochemical processes (Bu'Lock 1965).

As to their nutritional quality for herbivores there is reason to believe that green plants are much more variable than previously thought (Fraenkel 1953). The recognition of so called 'C₄ plants' with high photosynthetic capacity and 'C₃ plants' with low photosynthetic capacity raises the possibility for differences in the nutritional value of plants to be founded on deeper physiological reasons (Black 1971). It appears that in general 'C₄' species are a poorer food source for herbivores than 'C₃' species (Caswell et al. 1973).

The diversity of insect/plant interactions cannot be explained by one universal model. It seems now generally accepted that these interactions are mediated by nutrients as well as by compounds of the secondary plant metabolism. These compounds acting as allelochemics may either provide an adaptive advantage to the plant (allomones) or provide an adaptive advantage to the insect (kairomones). All sorts of purely qualitative, quantitative, synergistic, and antagonistic effects have been detected among the multitude of plant compounds implicated in host-selection processes. The basic behavioral and physiological processes mediated by these compounds are host-finding for feeding and oviposition by the adult female, and host-finding for feeding, growth and development of immature stages.

Generalized Host-plant Selection Process

A complex sequential process such as host-plant selection is better described as a chain of events (Thorsteinson 1960). The classical phases of host-selection, rather anthropomorphically named: host-habitat finding, host-finding, host-recognition and acceptance, and host-suitability (Kogan and Goeden 1971) are linked in a flow diagram (Figure 2) in which plant and environmental inputs are represented as trapezoids, insect's behavioral or physiological patterns as rectangles, and 'decision steps' as diamonds. The generalized chain of insects in host plant selection is described in the caption of Figure 2.

Table 1.—Generalized relationship between allomones, and kairomones and fundamental insect responses.¹

Plant chemical factors	Insect response					
	Adult			Larvae		Growth and development
	Host-finding	Feeding	Oviposition	Host-finding	Feeding	
Attractants	G.R.S.	N	N	G.R.S.	N	N
Repellents	G.R.S.	N	N	G.R.S.	N	N
Arrestants	G.R.S.	N	N	G.R.S.	N	N
Excitants	N	G.R.S.	G.R.S.	N	G.R.S.	G.R.S.
Supressants & Deterrents	N	G.R.S.	G.R.S.	N	G.R.S.	N
Antibiotics	N	G.R.S.	N	N	G.R.S.	G.R.S.
Nutrients	N	G.R.S.	G.R.S.	N	G.R.S.	G.R.S.

¹ G.R.S. — Factors with General (G), Restricted (R), or Specific (S) occurrence: N — no effect of this factor on given insect response.

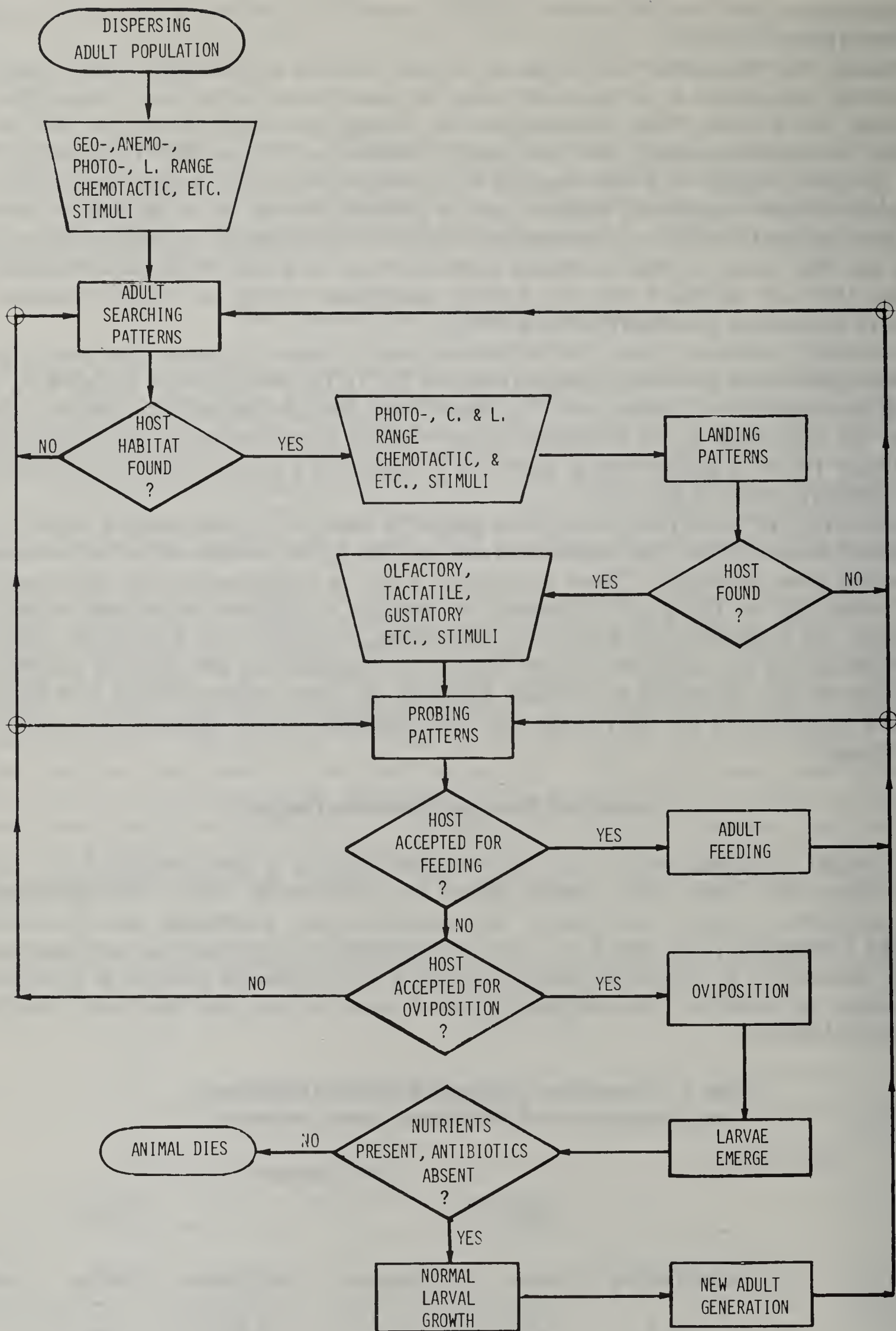


Fig. 2. —Flowchart of a generalized host-selection process. Dispersing adult populations respond to physical and chemical stimuli of the environment (upper trapezoid) and initiate a searching pattern that leads to the host's habitat. If the habitat is found (upper-left diamond) the process proceeds in successive steps contingent on the presence of proper stimuli. Successive phases of the process include host-finding, acceptance, initiation and maintenance of feeding and/or oviposition. If the larval food contains proper nutrients and does not contain antibiotics development is completed and a new adult generation emerges. This new adult generation may resume the host-selection process at any pattern (rectangles) level following the phenology of the species. If the larval food is not adequate (nutritionally deficient, or containing antibiotics) larvae most likely die.

We may now conceive all possible qualitative and quantative combinations of plant chemical factors for simplicity indicated as compounds of general (G), restricted (R), or specific (S) distribution among the angiosperms (Table 1). The conceivable number of compounds and their combinations intervening at the various levels of the host-selection processes indicated in Figure 2 offer an almost unlimited number of possibilities which are certainly enough to account for the diversity of the insect/plant interactions observed in nature.

Plant Allelochemics in Insect/Plant Interactions

Many compounds have been positively identified with specific phases of the host-selection process. Extensive, although not exhaustive, tables were presented in recent reviews (Hedin et al. 1974, Schoonhoven 1972). Table 2 was extracted mainly from these reviews with the addition of a few more recently published data. The insect/plant systems are reported at the level of family, so that some degree of generalization can be achieved. Only specific compounds are included, although much more information is available on some active plant fractions extracted with solvents but with little additional chemical characterization. Bark beetles were also excluded so that focus could be placed mainly on leaf-feeding insects. Figure 3 gives the structural formulas of the isoprenoids listed on Table 2 to illustrate the vast range of chemical diversity and complexity of allelochemics implicated in host-plant selection.

Table 2.—Synopsis of plant chemical factors and their activity in insect/plant interactions.¹

Compounds of the primary metabolism and their polymers.

Chemical sp.	Effect	Insect/Plant System
CARBOHYDRATES		
Glucose	Feeding Excit.	Acrididae/Gramineae Epilachninae/Leguminosae Plutellidae/Cruciferae Pyrrhocoridae/Malvaceae
Fructose	Feeding Excit.	Acrididae/Gramineae Bombycidae/Moraceae
Maltose	Feeding Excit.	Acrididae/Gramineae
Sucrose	Feeding Excit.	Acrididae/Gramineae Bombycidae/Moraceae Chrysomelidae/Solanaceae Epilachninae/Leguminosae Pyrrhocoridae/Malvaceae Sphingidae/Solanaceae
Raffinose	Feeding Excit.	Acrididae/Gramineae
Cellulose	Feeding Excit.	Bombycidae/Moraceae
LIPIDS		
β-sitosterol	Feeding Excit.	Bombycidae/Moraceae
Phosphatidyl-Inositol	Feeding Excit.	Acrididae/Gramineae
Lecithin	Feeding Excit.	Acrididae/Gramineae
ORGANIC N-COMPOUNDS		
Ala+Ser+γ-Amino Butyric Acid	Feeding Excit. (at 8x10 ⁻⁴ M) Feeding Deter. (at .5M)	Acrididae/(Various)
Mono-Na Glutamate	Feeding Excit.	Acrididae/(Various)
γ-Amino Butyric Acid	Feeding Excit.	Chrysomelidae/Solanaceae
Alanine	Feeding Excit.	Chrysomelidae/Solanaceae

Chemical sp.	Effect	Insect/Plant System
Adenine-Chloride	Feeding Excit.	Curculionidae/Leguminosae
Adenosine	Feeding Excit.	Curculionidae/Leguminosae
ORGANIC ACIDS		
Oxalic Acid	Feeding Excit.	Chrysomelidae/Polygonaceae
Oxalacetic Acid	Feeding Excit.	Acrididae/Gramineae
Citric Acid	Feeding Excit.	Acrididae/Gramineae
	Feeding Deter.	Curculionidae/Cruciferae, Umbelliferae
α -Ketoglutaric Acid	Feeding Excit.	Curculionidae/Malvaceae
Malonic Acid	Feeding Excit.	Curculionidae/Malvaceae
Formic Acid	Feeding Excit.	Curculionidae/Malvaceae
Lactic Acid	Feeding Excit.	Curculionidae/Malvaceae
ℓ -Malic Acid	Feeding Excit.	Curculionidae/Malvaceae
Succinic Acid	Feeding Excit.	Curculionidae/Malvaceae
Ascorbic Acid	Feeding Excit.	Acrididadae/Gramineae
Compounds of the secondary metabolism		
ACETOGENINS AND PHENYLPROPANES ²		
<i>N-Aliphatic Alcohols and Aldehydes</i>		
β - γ -Hexenol	Attractant	Bombycidae/Moraceae
α - β -Hexenal	Attractant	Bombycidae/Moraceae
		Curculionidae/Cruciferae, Umbelliferae
<i>Flavonoids</i>		
Quercetin	Feeding Excit.	Curculionidae/Malvaceae
Isoquercitrin	Feeding Excit.	Bombycidae/Moraceae
Morin	Feeding Excit.	Bombycidae/Moraceae
7- α -L-Rhamosyl, 6-Methoxyluteolin	Feeding Excit.	Chrysomelidae/Amaranthaceae
Rutin	Feeding Excit.	Noctuidae/
<i>Quinones</i>		
Hypericin	Feeding Excit.	Chrysomelidae/Guttiferae
MBOA and DIMBOA ³	Feeding Deter.	Pyralididae/Gramineae
<i>Tannins</i>		
Tannins	Feeding Excit.	Acrididae/Rosaceae, Ericaceae
	Antibiotic	Lasiocampidae/Fagaceae Geometridae/Fagaceae
<i>Phenylpropanes</i>		
Coumarin	Attractant Arrestant & Feeding Deter.	Curculionidae/Leguminosae Curculionidae/Cruciferae, Umbelliferae
Chlorogenic A.	Feeding Excit.	Chrysomelidae/Solanaceae
Vanillin	Feeding Excit.	Curculionidae/Malvaceae
p-Methyl Acetophenone	Attractant & Feeding Excit.	Crambidae/Gramineae
ISOPRENOIDS		
Methyl Chavicol	Attr. & F. Excit.	Papilionidae/Umbelliferae

Anethole	Attr. & F. Excit.	Papilionidae/Umbelliferae
Carvone	Attr. & F. Excit.	Papilionidae/Umbelliferae
Coriandrol	Attr. & F. Excit.	Papilionidae/Umbelliferae
	Attractant	Bombycidae/Moraceae
Citral	Attractant	Bombycidae/Moraceae
Terpinyl Acetate	Attractant	Bombycidae/Moraceae
Linalyl Acetate	Attractant	Bombycidae/Moraceae
α -Pinene	Attractant	Curculionidae/Malvaceae
Limonene	Attractant	Curculionidae/Malvaceae
Caryophyllene Oxide	Attractant	Curculionidae/Malvaceae
<i>Triterpenes</i>		
Curcubitacins	Arrest. & F. Excit.	Chrysomelidae/Cucurbitaceae
Azadirachtin	Feeding Deter.	Acrididae/(Various)
<i>Bisterpenes</i>		
Gossypol	Antibiotic	Curculionidae/Malvaceae
ALKALOIDS		
<i>Lupin Alk.</i>		
Lupinine	Antibiotic	Aphididae/Leguminosae
	Antibiotic	Acrididae/(Various)
Lupanine & Hydroxydes	Antibiotic	Aphididae/Leguminosae
<i>Pyrrolizidine alk.</i>		
Nicotine	Antibiotic	Chrysomelidae/Solanaceae
Nornicotine	Antibiotic	Acrididae/(Various)
<i>Steroidal alk.</i>		
Solanine	Antibiotic	Acrididae/(Various)
Tomatine	Antibiotic	Acrididae/(Various)
	Antibiotic	Chrysomelidae/Solanaceae
Demissine	Antibiotic	Chrysomelidae/Solanaceae
<i>Tropane alk.</i>		
Scopolamine	Antibiotic	Chrysomelidae/Solanaceae
Atropine	Antibiotic	Chrysomelidae/Solanaceae
<i>Other alk.</i>		
Capaisin	Feeding Deter.	Chrysomelidae/Solanaceae
Nicandrenone	Feeding Deter.	Chrysomelidae/Solanaceae
CYANOGENETIC AND OTHER GLYCOSIDES		
Isothiocyanate	Feeding Excit.	Aphididae/Cruciferae
Glucosides ⁴	Attractant	Chrysomelidae/Cruciferae,
		Capparidaceae,
		Tropaeolaceae, &
		Limnanthaceae
	Attractant	Curculionidae/Cruciferae
	Attract. & F. Excit.	Plutellidae/Cruciferae
	Feeding Excit.	Lasiocampidae/Rosaceae
	Feeding Excit.	Epilachninae/Leguminosae
Amygdalin		
Phaseolunatin		
(+Glucose)		
Phaseolunatin	Feeding Deter.	Epilachninae/Leguminosae

Chemical sp.	Effect	Insect/Plant System
Calotropin	Feeding Excit.	Acrididae/Asclepiadaceae
Catalposide	Feeding Excit.	Sphingidae/Bignoniaceae

¹ Based mainly on Schoonhoven (1972), Hedin et al. (1974), and Beck and Reese (1976).

² See figure 3 for structural formulas.

³ MBOA = 6-methoxybenzoxazolinone

DIMBOA = 2,4-dihydroxy-7-methoxy-1,4-benzoxazine-3-one.

⁴ See table 4 for examples of most commonly found isothiocyanate glucosides.

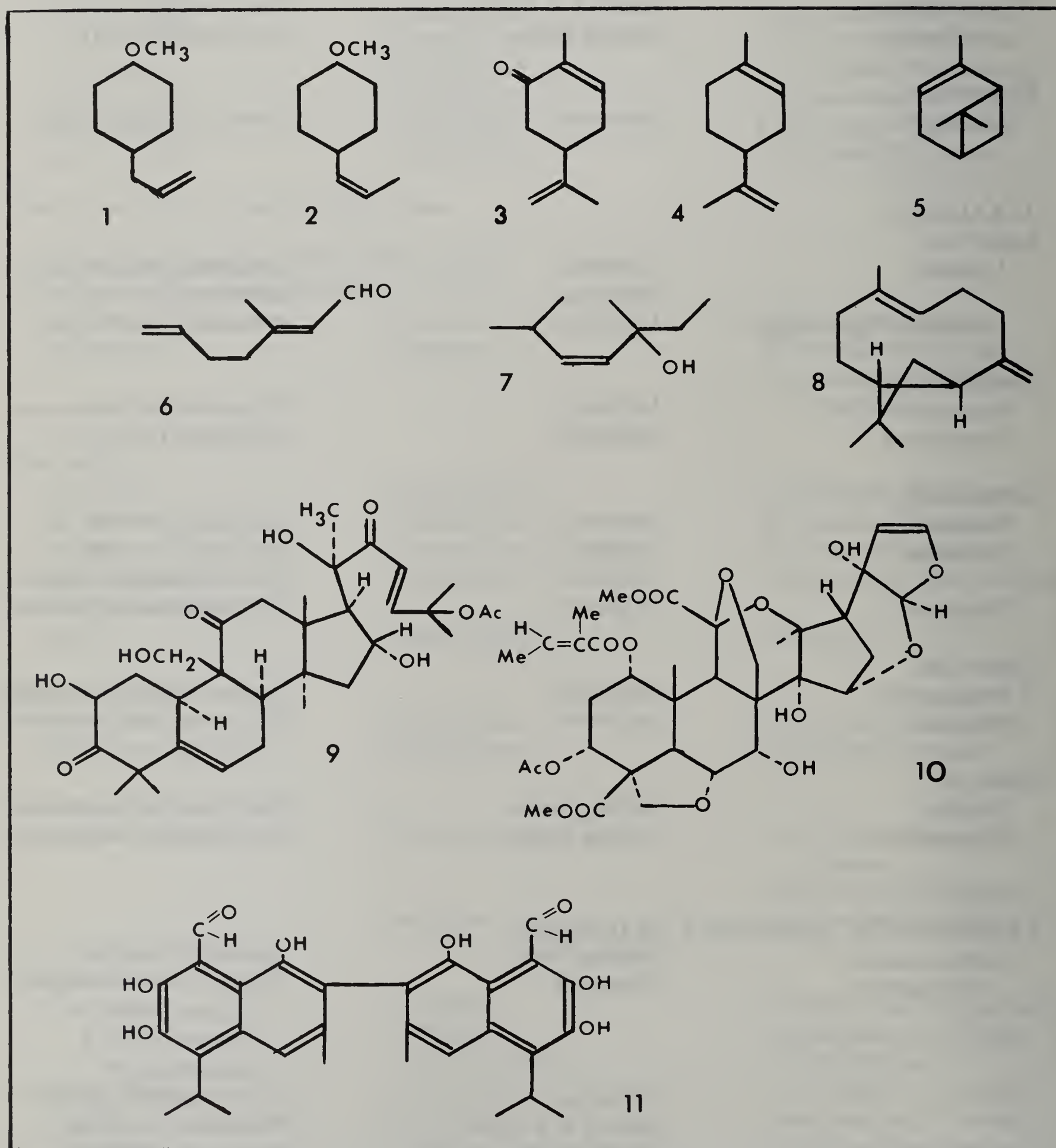


Fig. 3. —Structural formulae of some isoprenoids included in Table 2 illustrating the great diversity of plant compounds involved in insect/plant interactions. 1. Methyl chavicol, 2. anethole, 3. carvone, 4. limonene, 5. α -pinene, 6. eitral, 7. coriandrol, 8. caryophellene, 9. eucurbitacin A, 10. azidarachtin, 11. gossipol.

Chemical Bases of Host-selection Strategies

Behavioral and electrophysiological evidence for the allelopathic activity of plant products in insect/plant interactions is rapidly accumulating. It is, however, disturbing that the underlying chemical bases of only a few insect/plant interactive systems have been completely or nearly completely elucidated. Particularly deficient is our knowledge on host-finding by ovipositing females and the chemical regulation of oviposition selection. Yet, most authors recognize that oviposition is unquestionably the key step in most host-selection processes.

With the information gathered to date, however, we can begin to outline a few basic strategies in host-plant selection. The following is an attempt at describing six rather distinct models of host-selection strategies. Examples for these models were drawn from the best known insect/plant interactive systems. The models are presented from the more generalized to the more complex and specialized. Table 3 summarizes the main features discussed in the six models.

Model I

Oviposition is not selective. There is little or no influence of plant factors on oviposition behavior of adult females resulting in eggs being scattered in the habitat or laid on some non-plant substrate. Adults and immature stages follow similar patterns in food-plant selection. Orientation to food plant is triggered by generalized mechanisms (photo- and anemotaxis). Plant recognition usually involves contact chemoreception. Host-acceptance results from the presence of feeding stimulants of universal occurrence (sucrose, lipids, vitamins) and absence of a few extremely active deterrents of rather restricted distribution. Highly polyphagous species.

Example. — Several polyphagous species of Acrididae follow this model. Eggs are laid in the soil although different species may require somewhat different conditions for oviposition. Random movements elicited by hunger, warm temperature, and light (Mulkern 1967) or positive anemotaxis possibly reinforced by plant odors (Kennedy and Moorhouse 1969) bring the grasshopper into visual range of vertical objects. Upon climbing the object the animal bites into the edge and feeding proceeds if excitants are present. Feeding excitants positively identified include glucose, sucrose, phospholipids, lipid mixtures, ascorbic acid, thiamine, among others (Mulkern 1967). The host-plant range is limited only by very potent deterrents of rather restricted occurrence. An example of such deterrents are the triterpenoids azadirachtin (Figure 3), and meliantrial (Nakanishi 1975) from the Meliaceae, *Azadirachta indica* — a plant that is virtually free of herbivorous enemies.

Model II

Long-range chemical attractants are not present. Short-range attractants, if present, are not specific. Specific close-range repellents may be present. Colonizing adult populations perform as r-strategists constituting a considerable contingent of the arthropod aerial plankton. Landing is elicited by visual cues. Landing on plants at random is followed by probing of the landing sites. Sojourn on the landing site depends on the presence of arrestants. Arrestants and oviposition excitants are ubiquitous compounds (water, sucrose, amino acids). Immature stages usually accept and complete development on a wide variety of food-plants which are selected by the colonizing adults. The relative distribution of antibiotic factors determines the nature of the host-plant range.

Example. — This model is probably followed by most polyphagous aphids, whiteflies and thrips. Some polyphagous aphids, such as *Myzus persicae* (Sulzer) and *Aphis fabae* Scopoli, alight on objects reflecting maximally above 500 m μ (green-yellow-orange) (Kennedy et al. 1961). There is however, some evidence that landing of *M. persicae* alatae may not be completely indiscriminate since certain plants or leaves may be avoided indicating that close range repellents may be present in certain non-hosts (van Emden et al. 1969). Probing follows landing and in *M. persicae* discrimination of physiological state prevails over plant taxonomy. On some hosts aging or senescing leaves are preferred whereas on others the aphids prefer young or growing leaves.

Continuous adult feeding and progeny production are determined by the nutritional adequacy of the host. On artificial diets *M. persicae* prefers sucrose + amino acids solutions > sucrose > water.

It seems that sinigrin, a mustard oil glucoside, deters feeding by *M. persicae*. It is possible that the selection of old or senescing leaves of crucifers is correlated with lower concentrations of glucosides in these leaves (van Emden et al. 1969).

Table 3.—Host-selection strategies in six insect/plant interactive systems.

HOST SELECTION PROCESSES						
Model	Adult Oviposition	Host-Finding	Larvae	Host-Plant		
				Feeding ¹	Range	System
I	Non-selective; ovip. on non-plant substrates.	Active search, G. attractants ¹		G. excitants R. deterrents	Adult=Larvae	Polyphagous Acrididae/Angiosperms
II	Ovip. on plant substrate after selective probing.	Passive ²		G. excitants R. deterrents	Adult=Larvae	Polyphagous aphids/Dicotyledoneae
III	Non-selective; ovip. on non-plant substrate.	Active search (root feeders) probably G. attractants		(unknown)	Adult≠Larvae	Diabroticites/Cucurbitaceae/Gramineae
IV	Ovip. on selected plant substrates.	Passive		G. excitants S. deterrents	Adult=Larvae	Chrysomelidae/Solanaceae
V	Ovip. on selected plant substrates.	Passive		S. excitants	Adult=Larvae	Cruciferae associated species
VI	Ovip. on selected plant substrates.	Passive		S. excitants S. deterrents	Adult≠Larvae	Heliconius/Passiflora/Cucurbitaceae

¹ Compounds of general (G) restricted (R) or specific (S) occurrence.

² Immature stages emerge on host-plant.

Model III

Adult host-finding behavior for feeding probably follows a random pattern. An appropriate food source produces strong, specific arrestants and feeding excitants but weak attractants. The first colonizers start feeding and produce a potent aggregation pheromone inducing an oriented flight pattern that results in large numbers of individuals concentrating on the food source. Oviposition is not selective and eggs are laid in non-botanical substrates. Larvae live in a different environment than adults and feed on different hosts.

Example. — Several species of *Diabrotica* and *Acalymma* (Coleoptera: Chrysomelidae) display considerable preference for species of Cucurbitaceae, in particular those with high cucurbitacin concentrations. Several authors have suggested that cucurbitacins acted as attractants. Results of their bioassays suggested that cucurbitacins were potent arrestants and feeding excitants rather than attractants. Host-finding would, therefore, result from random search or possibly by following visual cues, although the existence of other attractants should not be ruled out. Upon landing on a cucurbit beetles would be arrested and excited to feed by action of the cucurbitacins. Following initial feeding by the first colonizers an aggregation pheromone would be produced. Thereafter, host-finding would be oriented by the pheromone source. Such a host-selection mechanism is similar to that of bark beetles. An adaptive advantage of such a mechanism would be that ingestion of the bitter cucurbitacins may provide a defense mechanism against vertebrate predators; by virtue of the aggregation pheromone a greater proportion of the beetle population would more rapidly acquire the bitter taste thus enhancing its protective effect (Howe et al. 1976).

Little is known about food selection behavior of the larvae. They are root feeders and eggs are laid in the soil. There seems to be little effect of soil coverage by plants on oviposition behavior of the adults. Oviposition, therefore, is not selective.

Model IV

Host-finding for oviposition is directional. Adult females display positive anemotaxis if plant odours diffuse in the air-current. Contact chemoreceptors permit a high degree of discrimination and oviposition is usually made on suitable host plants. Larvae are less discriminatory and, do not seem to require specific feeding excitants. Restrictions on the host-plant range are imposed by the nature of feeding deterrents, rather than the presence of excitants. They are usually oligophagous species which acquire some degree of protection from predation due to accumulation of plant antibiotic factors. Insect species in these associations evolved mechanisms to sequester, by-pass, or detoxify the host plant's antibiotic defense factors.

Example. — A complex of three insect species, *Lema trilineata daturaphila* Kogan and Goeden, *Leptinotarsa decemlineata* (Say), and *Manduca sexta* (L.), associated with solanaceous hosts typify this model. Oviposition tests with all three species indicate a high degree of discrimination by the adult female (Force 1966, De Wilde et al. 1969, Yamamoto et al. 1969, Yamamoto and Jenkins 1972). Larvae are less discriminating, and their potential host-range is broader than the actual host-range. Larvae in the laboratory can be made to feed and complete development on plants never fed upon in nature.

Yamamoto (1974) has shown that first instars of *M. sexta* are rather polyphagous and accept various non-solanaceous plants including some Scrophulariaceae, Cruciferae, Moraceae, Plantaginaceae, and Leguminosae. Similarly, *L. decemlineata* larvae are more broadly selective for feeding than the adults are for oviposition, as they fed and grew on plants of the Leguminosae, Cruciferae, Compositae, and Asclepiadaceae (Hsiao and Fraenkel 1968). *L. trilineata* larvae seem to be more host-specific at the larval stage than the other two species. Only moderate feeding, but no development, was recorded on one plant, a crucifer, outside the normal host-plant range (Force 1966).

The host-plant ranges of the three species in this system include solanaceous plants characterized by the presence of certain classes of alkaloids. *Lema trilineata* feeds mainly on *Datura* spp. and certain species of *Physalis*, *Atropa*, *Nicandra*, and *Salpichroa* (Kogan and Goeden 1970) all characterized by the presence of tropane alkaloids (Hegnauer 1973). *Leptinotarsa* is primarily associated with *Solanum tuberosum*, the potato plant, and a few other species of *Solanum* and *Lycopersicon*, which are characterized by the presence of certain steroidal alkaloids or their parent glycosides, such as α -solanin, and α -chaconin (Schreiber 1958). *M. sexta*, is primarily associated with

tobacco and tomato, but accepts other solanaceous plants, including *Datura*, *Physalis*, *Hyoscyamus*, and *Atropa* (Yamamoto and Fraenkel 1960). The ability of *M. sexta* to utilize these plants suggests that it is endowed with broad-spectrum tolerance to some highly toxic alkaloids, including steroidal, tropane, as well as nicotine, a pyrrolizidine alkaloid.

From all indications no specific or even restricted feeding excitants have so far been demonstrated in the solanaceous hosts of the species. These compounds include sugars, phospholipids, certain amino acids, flavonoids and certain phenolic compounds of wide distribution among the angiosperms and could not, by themselves account for the oligophagy in this species complex. The differential susceptibility of these species to the various classes of alkaloids of the solanaceae seem to offer the clue for their selectivity of host-ranges. Detoxication or excretion mechanisms are found in the three species. *L. trilineata* tolerates injection into the homocoel of .25 and .50 mg of scopolamine hydrobromide per larva; tropane alkaloids contained in *Datura* leaves were recovered in nearly quantitative amounts from the feces of *Lema* larvae, suggesting also existence of an effective excretory mechanism (Kogan and Goeden 1971). *M. sexta* apparently has a high tolerance for nicotine-producing plants which is facilitated, at least in part, by an efficient excretion of nicotine (Self et al. 1964a, b). The toxicology of steroidal alkaloids in *Leptinotarsa* was investigated by several authors and the inhibitory affect on feeding and growth of demissin and tomatin were reported as resistance factors in certain solanaceous species (de Wilde 1958). It seems, therefore, that the host-ranges of these three species of insects associated with the solanaceae are defined by the distribution of certain classes of alkaloids. *Leptinotarsa* can tolerate certain steroidal alkaloids but is susceptible to tropane and other (nicotine, nicandrenone) alkaloids; *Lema*, is susceptible to nicotine and most steroidal alkaloids but tolerates the tropane group, *M. sexta* in turn must be able to handle equally well alkaloids of the three classes since several tropane, nicotine, and steroidal alkaloid containing plants are included in its host-range. This host-selection mechanism can operate with efficacy only if the ovipositing female has the sensorial capability of discriminating among the various alkaloid type plants. This capability has yet to be demonstrated. However, the greater selectivity of ovipositing females of these species provides some indirect evidence.

Model V

Host-finding for oviposition and feeding are highly selective. Larval feeding is also selective and the biochemical basis of host-plant selection is the same for adults and larvae. Specific attractants, and feeding and oviposition excitants are characteristic of the plants in the host-range. Mostly oligophagous species.

Example. — It seems that most Cruciferae-associated species are attracted and excited to oviposit by the characteristic isothiocyanates or their parent glucosides of that plant family. These same compounds attract and elicit feeding responses in larvae. Sinigrin, allyl-isothiocyanate glucoside, is one of the most widely distributed compounds of this group. But its own concentration and the relative concentration of other isothiocyanates vary among the different species of Cruciferae (Tables 4 and 5). Consequently the various species of Cruciferae are differentially preferred by the various species of insects tested. It is also possible that additional feeding excitants are required or that feeding deterrents are present that override the excitatory effect of the isothiocyanates, since certain species are rejected by cruciferous associated insects despite the fact that they contain adequate amounts of isothiocyanates or their glucosides (Feeny et al. 1970).

Several insect species have been studied in their relationship with the Cruciferae and other isothiocyanate containing plant families. The number of species involved and the fact that all major taxa of phytophagous insects have representatives closely associated with these plants is an indication of how successful this host-selection process has been among insects. Examples of this association are: Diptera — *Erioachia brassicae* (Bouche) (Coaker and Finch 1973); Lepidoptera — *Pieris* spp. (Hovanitz 1969), *Plutella maculipennis* (Curt.) (Thorsteinson 1953, Nayar and Thorsteinson 1963); Coleoptera — *Listroderes costirostris obliquus* (Klug) (Matsumoto and Sugiyama 1960), *Phaedon cochlearia* (F.) (Tanton 1965), *Phyllotetra cruciferae* and *P. striolata* (F.) (Feeny et al. 1970); Homoptera — *Brevicoryne brassicae* (L.) (Wensler 1962). This model is a classified example of the undisputed role of natural plant products as attractants and oviposition and feeding excitants. The coevolutionary features of this system are enhanced by the fact that mustard oil glucosides may be deterrents to other herbivores, and that these chemicals are sequestered and act as feeding deterrents to predators. For example, *Pieris brassicae* stores allyliosothiocyanate in eggs, pupae and adults, which are rejected by certain predators (Aplin et al. 1975).

Table 4.—Occurrence of some isothiocyanate glucosides in select species of Cruciferae.¹

Plant Species	Common Name	Part ²	Compounds ³
<i>Brassica juncea</i>	—	R G	Gluconasturtiin Sinigrin, Gluconapin, Glucobrassicinapin, Gluconasturtiin
<i>B. nigra</i>	—	G	Sinigrin, Gluconasturtiin
<i>B. oleraceae</i> var. hort.	—	G	Sinigrin, Gluconapin, Glucoibervirin, Glucoiberin, Glucoraphanin, Progoitrim
<i>Dentaria digitata</i>	—	G	Glucocapparin
<i>Erysimum cheiranthoides</i>	Wormseed-mustard	G	Glucocochlearin, Sinigrin
<i>Hesperis matronalis</i>	Dames violet	G	Glucocapparin, Glucolepidin Sinigrin, Glucoputranjivin
<i>Iberis amara</i>	Candy tuft	G	Glucoiberin
<i>Lepidium campestre</i>	Cow cress	G	Sinalbin
<i>Raphanus sativus</i>	Radish	R	Glucoputranjivin, Glucoraphenin
<i>Sisymbrium officinale</i>	Hedge mustard	G	Glucocapparin

¹ Based on Kjaer (1960)

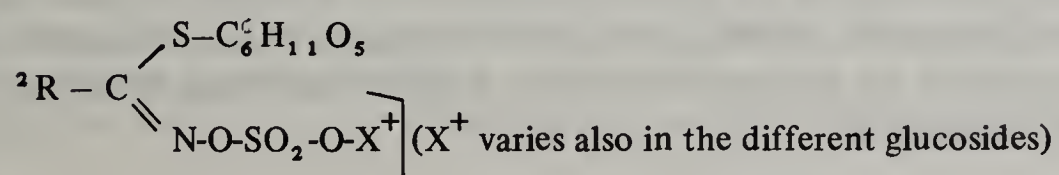
² R—roots, G—general aerial parts

³ See chemical structure in Table 5.

Table 5.—Isothiocyanate glucosides occurring in the cruciferous plants listed in table 4.¹

Parent Glucoside ²	R
Glucocapparin	CH ₃
Glucolepidin	CH ₃ CH ₂
Glucoputranjivin	CH ₃ CH(CH ₃)
Glucocochlearin	(+)-CH ₃ CH ₂ CH(CH ₃)
Sinigrin	CH ₂ =CHCH ₂
Gluconapin	CH ₂ =CHCH ₂ CH ₂
Glucobrassicinapin	CH ₂ =CHCH ₂ CH ₂ CH ₂
Glucoibervirin	CH ₃ SCH ₂ CH ₂ CH ₂
Glucoiberin	CH ₃ SOCH ₂ CH ₂ CH ₂
Glucoraphanin	CH ₃ SOCH ₂ CH ₂ CH ₂ CH ₂
Glucoraphenin	CH ₃ SOCH=CHCH ₂ CH ₂
Gluconasturtiin	C ₆ H ₅ CH ₂ CH ₂
Progoitrim	CH ₂ =CHCHOHCH ₂

¹ Based on Kjaer (1960)



Adult behavior in host-finding for feeding and oviposition is highly selective. The host-plant ranges of adults and larvae are very different and consequently so are the selection mechanisms involved. Complex sensorial mechanisms permit adult females to locate larval host plants for oviposition and their own hosts for feeding. These mechanisms are visual as well as tactile and chemotactic, and there is evidence that a learned associative behavior is involved.

Example. — The classical example for this model is provided by the Heliconidae/Passifloraceae/Cucurbitaceae system, the complexities of which have been summarized by Gilbert (1975). Adult *Heliconius* seem to have a mutualistic relationship with cucurbits of the genera *Anguria* and *Gurania*. Mechanisms for host-finding are not completely elucidated but Gilbert indicates that foraging becomes more efficient with age and that learning may be involved in the location of pollen and nectar sources. Host-selection for oviposition involves a major visual component but *Passiflora* species are known to contain saponins, alkaloids, and phenolic and cyanogenetic glucosides that may have some allelochemic effect. Female *Heliconius* were reported to tap candidate plants for oviposition with their forelegs which are endowed with contact chemoreceptors. *Heliconius* eggs are seldom found on unsuitable hosts (Benson et al. 1975). Larval feeding behavior seems to have evolved also a very high degree of discrimination. For instance Mexican populations of *Eueides isabella* refuse to feed on new growth of *Passiflora serratifolia*, although they feed and develop on older leaves. Young growth of this plant is toxic to larvae from other populations of *E. isabella* that have not evolved a discriminatory mechanism and do not reject feeding on the plant (Benson et al. 1975).

Concluding Remarks

The analytical interpretation of insect/plant interactions has a sound conceptual foundation in the coevolutionary theory of animals and plants (Gilbert and Raven 1975). Insect/plant interactions are part of the complex framework of community ecological phenomena, consequently the full realization of an insect's feeding niche involves many biotic and abiotic components of the ecosystem. One consequence of adopting the coevolutionary analytical approach is that researchers must attempt to find explanations for these interactions beyond the more obvious regulatory effects of a few plant natural products on displays by insects of a modest repertoire of stereotyped behaviors. All secondary ecological benefits an insect derive from feeding on a plant are paramount in the reinforcement of a feeding habit but as a first necessary step the animal must start eating that plant. The advantage that the monarch butterfly larvae derives from feeding on the poisonous milkweeds could only manifest itself after the animal first fed on that plant. The central role of plant allelochemicals in the initiation and maintenance of these feeding habits is now unquestionable (Beck and Reese 1976).

Much of the research on host-plant selection was centered on temperate zone insect species feeding on annual crop plants. The research on *Heliconius* is evidently an exception. In the models described above the connection between the insect and its food plant is cyclically interrupted by virtue of the completion of the plant's annual cycle or by the advent of winter that forces insects into a temporary abandonment of the spatial contact with the host. Under these circumstances mechanisms that assure reestablishment of spatial contact are the key in host-plant selection, hence the importance of host-finding by ovipositing females. Despite the fact that most researchers recognize that the ovipositing female is the key to unraveling some crucial phases of the host-selection process, amazingly little is known on allelochemic effects on host-finding and oviposition behavior. The female ovipositor of many phytophagous insects is endowed with several types of sensilla. However, to my knowledge, very little has been done electrophysiologically or behaviorally to assess the role of these sensilla.

The subsequent phases of the host-selection process were more intensively investigated. The picture that is slowly emerging is that the food plant of an insect is not a mosaic of strong, independent stimuli, derived from odd plant molecules, the mustard oils notwithstanding. The food plant accepted for feeding by the larvae and suitable for the animal's growth and development is an integrated chemical entity probably perceived as a total "Gestalt." Investigations oriented at revealing synergistic or antagonistic interactions of allelochemicals should improve definition of this integrated chemical entity. Existing bioassays are still too crude to detect subtle influences of pure chemicals, and particularly the synergistic or antagonistic effect of mixtures. Better bioassays will be needed in the investigation of these influences.

According to Emlen (1973) selection favors maximum efficiency in feeding. The recognition of certain basic models in insect's host-selection processes suggests that insects have found several solutions to maximize feeding efficiency. There is little doubt that additional models will be recognized as more is learned about the effect of natural plant products on insect feeding, nutrition, and host selection behavior. The reference to models is an attempt to stress the diversity and complexity of the chemically mediated insect/plant relationships. The bulk of the information available on host-selection processes is based on studies of a very few insect/plant systems. Table 2 shows only 18 plant families (out of about 320 existing families of angiosperms) with representative species investigated in their relationship to insects. As these investigations are expanded to include other systems it is obvious that many additional models will be identified.

The practical implications of the full elucidation of the chemical basis of host-plant selection processes of agricultural pests fully justify research efforts in this field. The identification of the chemical basis of host-plant resistance greatly improves the efficiency of programs for breeding resistant varieties. It would also open new avenues for the manipulation of insect's behavior for use in pest management programs. Although these practical applications must be recognized it is the fundamental scientific knowledge gained on one of the most fascinating aspects of the interdependence of organisms and their harmonic coevolution that makes the analysis of insect-plant interaction one of the most exciting areas of entomological research.

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Sensory Aspects of Insect Plant Interactions

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ABSTRACT

Insect plant interactions are reviewed in the light of studies based on electrophysiological recordings from sensory organs and ablation experiments in combination with behavior observations. Many investigations show that different senses including vision (color, shape) and mechanoreception (texture, shape) can be involved in different phases of plant-related behavior. With few exceptions it is clear that chemoreception is the dominant sense in insect plant interactions.

Contact chemoreceptive sensilla of honeydew and nectar-feeding insects contain receptor cells sensitive to many compounds including water, salts, sugars, acids, aminoacids etc. In the olfactory sensilla of these insects (adult Diptera, Hymenoptera, Lepidoptera) receptors have been identified responding to many "flower" odors such as different aliphatic and aromatic compounds, and various terpenes and their derivatives. In plant feeding insects (Acrididae, Lepidoptera larvae) olfactory receptor cells have been identified sensitive to known components of plant odors. The contact chemoreceptive sensilla styloconica of Lepidoptera and Coleoptera larva seem to be well adapted to the perception of the complex chemical composition of leaves including sugars, aminoacids, and various deterrents. Narrow specificity for typical (in the sense of chemotaxonomy) compounds has been identified only in larva living on Crucifera plants: mustard oil glucosides.

So far it seems that chemoreceptive cells of insects being attracted or stimulated (feeding, oviposition) by undamaged plants are more specific for "plant sign stimuli". Examples of receptors of mono- or oligophagous insects include antennal, olfactory cells specific for host plant typical terpenes (pine weevil), and tarsal contact chemoreceptors specific for mustard oil glucosides (*Pieris* female) and hypericin (*Chrysomela*).

Host plant specificity does not have to depend on chemoreceptor cells with restricted reaction spectra. Behavioral studies, and electrophysiological investigations of sensory and central interneurons have accumulated evidences for sensory coding by a cross fiber patterning. Sensory information of different modalities and qualities can allow insects to discriminate between distinct chemicals as well as between complex natural stimuli provided by host plants. Though limited, our knowledge of insect sensory physiology indicates that total sensory patterns are most important in all insect plant interactions. The difficulties and suggested solutions in studying elements of such sensory codes are discussed and the importance of future multidisciplinary research efforts is stressed.

Insect plant interactions are governed on one side by the physiological reactions of the plant and on the other by the sensory perception of the plant stimuli resulting in behavioral and physiological reactions of the insect (Kogan this vol.). Since sensory perception represents the link between plant and insect it is of primary interest. All sensory organs of the insect seem to be involved at least partially in the perception of plant stimuli. These are the compound eyes, ocelli, different mechanoreceptive sensilla, temperature receptors and chemoreceptive sensilla. Chemical factors of the plant seem to dominate the insect plant interactions (Kogan, Swain this vol.) and accordingly

chemosensory organs play a central role in this relationship. Consequently this review will show up the importance of the various chemoreceptive organs. It was attempted to concentrate on the sensory aspects of plant insect interactions. As a consequence behavior aspects had to be neglected insofar as no direct relation to sensory physiology could be deduced.

The first complete review of this subject has been presented by Schoonhoven (1968). Newer publications on sensory aspects of plant insect interactions have been presented by Schoonhoven (1972a, b, c, 1976) and Dethier (1973, 1974a, 1976).

Vision

(A) Color

Behavior responses (attraction, landing, feeding, and oviposition) of different phytophagous insects to yellow is a well-known fact (for examples see Moericke 1950, 1955, Nolte 1959, Kennedy and Booth 1961, Sternlicht 1974, Herger 1975, Moericke et al. 1975). Attraction toward yellowish hues can be explained as a positive response of insects to the reflectance between 520-600 nm which is the area of the insect visible spectrum where green leaves reflect their peak energy (Prokopy et al. 1975, Vaishampayan et al. 1975). So far only one example of a host plant specific color behavior by an aphid *Hyalopterus pruni* Goeffr. has been reported by Moericke (1969). This seems to be an exception since even the olive fly (*Dacus oleae* Gmelin), having a host plant with foliage different from the "normal" green of most plants, cannot discriminate between the color of host- and nonhost leaves (Prokopy et al. 1975).

The receptors for yellow light stimuli must be located in the compound eyes of adults and the ocelli of larvae (Meisner and Ascher 1973). Indeed in the locust, receptor cells have been found responding specifically to the green fraction of the visual spectrum with a peak response to 520 nm. Since these green receptors do occur together with UV receptors in the same cell it is not yet clear if and how this visual information is mediated to the brain (Bennett et al. 1967).

Flower-visiting insects such as the honey bee have been long known to respond to colors of flower petals (for review see Dethier 1963). In the eyes of these insects different color receptor cells (mainly UV and green) have been identified (Menzel 1975) and spectral sensitivity seems well matched with the proven discriminating abilities (Goldsmith and Bernard 1974).

(B) Visual Patterns

Only behavioral evidence exists for the influence of shape or form perception in insect plant interactions. So grasshoppers have been observed orienting to vertical objects (Mulkern 1969). This behavior is not unusual in insects (Jander 1971, Wehner 1975), and can explain an unspecific orientation toward plants. More specific visual responses to plant patterns (fruits) have been reported from different species of flies in the family Trypetidae (Tephritids). Zwölfer (1968) showed that *Urophora siruna-seva* Hg. males and females find their host, having a globular body with radially divergent spines, by means of visual stimuli. In other species attacking various fruits, males and females have proven to visit preferably spheres with a diameter and color corresponding to the natural host fruit (for review see Cirio 1972). The study of pattern perception mechanisms has been started in recent years. The results obtained are fascinating and do reflect the complexity of the central process involved in pattern recognition (Goetz 1975, Wehner 1975). Obviously much more has to be known before visual orientation of insects to plants can be explained by central perception mechanisms.

Mechanoreception

Mechanoreception may play a crucial role during some behavior phases but is inherently not very specific in regard to the plant. The distribution, structure and physiology of arthropod mechanoreception have been recently reviewed by Schwartzkopff (1974), McIver (1975), and Rice (1975).

Physiological studies did involve mainly ablation techniques of sensory organs (Yamaoka et al. 1971) and of nerves (Gelperin 1967, and Yamaoka and Hirao 1971, Bernays and Chapman 1973, Louveaux 1976). Electrophysiological recordings (Schoonhoven and Dethier 1966, Hanson 1970) can

prove the existence of a mechanoreceptive receptor-cell and provide results on its response to different adequate stimuli. But the function in the normal behavior can only be deduced from ablation experiments. Mechanoreceptors of plant feeding insects are probably involved in the monitoring of leaf geometry, the consistency of the leaf or portions thereof (Sinoir 1968, Heinrich 1971, Bernays and Chapman 1974) and are possibly providing information on the distance and contact between the leaf and the chemoreceptive sensilla (Staedler and Hanson 1975).

The mechanoreceptive sensilla on the ovipositor are necessary for the regular positioning of eggs in *Bombyx mori* L. (Yamaoka et al. 1971) but may be also involved in other insects in the perception of surface shape and texture as well as the internal consistency of the oviposition substrate (e.g., *Rhagoletis* species, see Boller and Prokopy 1976).

Proprioceptive sensory structures are widely distributed in the cuticle of arthropods (McIver 1975). Louveaux (1976) showed convincingly that such receptors located in the hypopharynx of *Locusta* are indispensable for coordinated movements during swallowing. However, it is uncertain that this proprioception involves any specific information on the leaf quality. Proprioceptors in the joints of legs could be envisaged as the possible sensory organs involved in kinesthetic perception of shape and surface structure of fruits and leaves (Prokopy 1968, Zwölfer 1968, Staedler 1971/72, 1976).

Regulation of feeding is controlled by a negative feedback mechanism provided by internal mechanoreceptors located in the crop of the locust (Bernays and Chapman 1973) and the crop and body wall in fluid feeders (reviewed by Gelperin 1971a, b).

It can be concluded that mechanoreceptors are indispensable for all behavior sequences including interaction with plants but the perceived stimuli seem to be mostly of secondary nature.

Temperature and Humidity Perception

In different insects, receptors have been described to be sensitive to temperature (for ref. see Davis and Sokolove 1975, Reinhouts van Haga and Mitchell 1975) and humidity (olfactory perception of water vapor, for ref. see Arbogast et al. 1972, Pinet & Bernard 1972). However, only few records are available of such receptors involved in insect plant relationships. The cold and humidity receptors of *Lepidoptera* larvae located in the antennae and maxillary palpi have been reported to be sensitive to changes in temperature and rel. humidity (Schoonhoven 1967a, Dethier and Schoonhoven 1968). These receptors allow for mediating information to the central nervous system about turgidity of leaves. Antennal sensilla of the locust respond to moisture as well (Waldow 1970), but there seems to be no evidence that these receptors influence feeding (Bernays and Chapman 1974).

Chemoreception

(A) Methods of Investigation

(1) Behavior observations. — The observation of the insect behavior in a close to natural situation is certainly an important prerequisite for any attempt of a complete analysis of insect plant relationships. However, the study of sensory aspects certainly need results from a lower level of integration, as exemplified by investigation of sense organs themselves.

(2) Ablation Experiments. — This approach has been widely used, and different techniques have been developed such as removing or cauterisation of complete organs and sensory organs, treatment of sensilla with acids, and cutting sensory nerves. Since any kind of ablation is prone to cause unwanted disturbance of the normal behavior (which is the indicator for the effect) special controls have been designed. So in paired organs unilateral amputations have been applied (e.g., Hanson and Dethier 1973). Sham operations can also give satisfactory control for the negative influence of injuries due to operations (e.g., Louveaux 1976).

The advantage of ablation experiments is that the elimination of the sensory input can be directly correlated to the behavior reaction of interest. The method is also indispensable in studies of the relative contribution of different sensory organs of the insect to the control of a specific behavior sequence (e.g., Ma 1972, 1976, Hanson and Dethier 1973, Blaney and Chapman 1970). However, despite the necessary controls any ablation technique has serious limitations: "Negative results,"

namely the lack or failing of a behavior response occurring normally in the control animals, can be not only the effect of the removed sensory input, but could be also a kind of irritation or reduction in the general activity.

(3) Morphology of Sensory Organs. — Any morphological data is of great importance as a prerequisite for electrophysiological recordings or as information for the interpretation of such results. For the study of the external morphology the use of the scanning electron microscope is ideal and has been widely used. Histological and ultrastructural details are more important and have been obtained using the light and electron microscope (for ref. Slifer 1970).

(4) Electrophysiological Recordings. — The monitoring of sensory nerve activity offers a direct approach to the identification and study of sensory aspects of insect plant interactions.

Contact chemoreceptive sensilla have been mainly investigated using the tip recording technique first described by Hodgson et al. (1955). In this method the stimulating solution in a glass capillary is used also as the recording electrode acting as an electrolytic bridge linked via an Ag/Ag Cl junction to the amplifier. The prime advantage of this technique is its simplicity. Disadvantages include the fact that nerve activity is only recorded during contact of the stimulus, the stimuli have to be water soluble, and that in most cases an electrolyte has to be added to the stimulating solution. The last named problem has recently been solved by Blaney (1975) using a very fine suspension of water insoluble, nonpolar waxes obtained through sonication. However, the difficulty remains that such suspended or emulgated compounds tend to reaggregate. Other problems concerning reproducibility will be discussed later.

The difficulties mentioned have been recognized long ago and a solution — the sidewall recording technique — has been developed. Morita and Yamashita (1959) first recorded by means of an artificial crack in the wall of gustatory hair sensilla of a blowfly. Rees (1968) refined this technique using glass microelectrodes inserted into the large lumen of the hair sensillum. Since certain sensilla can neither be cracked without damage nor inserted with glass electrodes Hanson (1970) introduced the use of tungsten electrodes.

Olfactory sensilla. — Summed activity in antennal nerves in response to some olfactory stimuli has been recorded first by Boistel and Coraboeuf (1953). From isolated, entire antenna slow potentials can be recorded representing integrated receptor potentials of all sensilla present which Schneider (1957) termed electroantennogram EAG. This technique can be readily applied to antennae of various insects. Despite the obvious limitations of the EAG due to the summed recording from different receptors this method has proven to be very useful for many applications (Schoonhoven 1974a). The combination of the EAG with high resolution GC (Arn et al. 1975) termed electroantennographic detector EAD has been developed for the analysis of pheromones but could easily be applied for the study of plant odor chemicals. The classical method for recording nerve activity from receptor cells of single sensilla has been developed by Morita and Yamashita (1961) and Boeckh (1962). Tungsten or glass capillary electrodes are inserted in the cuticle in the vicinity of the olfactory sensilla. Recently Kaissling (1974a) developed a new technique recording with nonpolarisable glass electrodes from the clipped tip of an olfactory sensillum trichodeum.

Problems arise mainly from the method of stimulation (cf. discussion Schneider 1968). Several solutions (with modifications) have been presented: (a) stimuli in varying concentrations on inert filter paper with time controlled air current delivered; (b) injection of compounds into constant air stream (Roelofs and Comeau 1971); (c) syringe technique: time-controlled air puffs saturated with stimuli dissolved in varying concentrations of paraffin oil (Kafka 1970); (d) direct use of the effluent of a gas chromatograph (Moorhouse et al. 1969, Arn et al. 1975).

None of the mentioned methods is ideal all having advantages and obvious disadvantages such as limited reproducibility or the fact that paraffin oil can be stimulating too (Sass 1976).

(B) Olfaction

Sinoir (1969a), Slifer (1970), Stuerckow (1970), Kaissling (1971, 1974b, 1976), Hodgson (1974) and Steinbrecht (1974a) described the distribution, morphology and general physiology of olfactory sensilla occurring on the antenna of imaginal insects such as *Sensillum trichodeum*, *S. basiconicum*, *S. coeloconicum*, *S. ampullaceum*, *S. placeodeum* and composed olfactory pits (*S. basiconica*). Maxillary palpi of flies bear also olfactory sensilla (van der Starre and Tempelaar 1976). The olfactory sensilla of Lepidoptera larva on the antennae and maxillary palpi have been described by Schoonhoven and Dethier (1966), Ma (1972) and Hanson and Dethier (1973). Olfactory sensilla

Table 1.—Perception of plant stimuli by olfactory receptors.

Abbreviations: El. phys.: Electrophysiological recordings of single sensilla
EAG : Electroantennnogram

Species	Perceived stimuli	Released behavior response	Investigation	References
<i>Antenna of imagines</i>				
<i>Diptera</i>				
Blowflies (Calliphora, Lucilia)	alcohols (C ₂ -C ₁₀) aldehydes (C ₄ -C ₁₀) fatty acids (C ₃ -C ₁₀) terpenes repellents	orientation to flowers?	El.phys.: pit organs EAG	Kaib (1974) Kay et al. (1967)
Hylemya brassicae Bouché	isothiocyanates	orientation to host plants	amputation EAG	cf. Dethier (1963) Coaker & Hawkes (1976)
<i>Hymenoptera</i>				
Apis mellifera L.	aliphatic hydrocarbons aromatic hydrocarbons bicyclic terpenes macrocyclic compounds	orientation to flowers	El.phys: s. placodea	Lacher (1964) Vareschi (1971) Kafka et al. (1973) Martin (1974)
Apoidea	extracts of blossoms sesquiterpene (q cadinene)	orientation to flowers	selective inhibition EAG	Priesner (1973)
Sirex noctilio F.	terpenes oxygenated terpenes	orientation to host plant	EAG	Simpson (1976) Simpson & McQuilkin (1976)
<i>Coleoptera</i>				
Bruchidae	plant odor	orientation to host?	EAG	Pouzat (1974)
Hylobius abietis L.	monoterpenes cyclohexenol benzene derivatives cyclic & aromatic hydrocarbons	orientation to host plant	El.phys: s. basiconica s. trichodea	Mustaparta (1975)
Scolytidae	carene, pinene	orientation to host plant	EAG	Payne (1970, 1975)

<i>Lepidoptera</i> Adris tyrannus amurensis Staudinger	host plant odors	orientation to plants	El.phys.: s. trichodea	Yamada (1970, 1971a)
	plant repellents	orientation to plants	EAG	
	host plant odors hexenal phenylacetylacetate terpineol hexenal	orientation to host plant	El.phys.: s. trichodea s. basiconica	Schneider et al. (1964)
Choristoneura fumiferana Clem.	host plant odors, pinene	sexual stimulation		Riddiford (1967)
Zeiraphera diniana Gn.	host plant odors	oviposition & oögenesis	El.phys. amputation	Albert et al. (1974) Staedler (1974)
	host and nonhost plant odors	orientation to host plant	amputation	Benz (1969) Altwegg (1971)
Hypsipula grandelle Zeller	flower odors hexenal	orientation to host plant	EAG	Schoonhoven (1974b)
Manduca sexta Johansen	host plant odors	orientation to flowers	EAG	Schoonhoven (1974b)
	host plant odors	orientation to host plant?	EAG	Schweitzer et al. (1976)
Plodia interpunctella Hübner	host plant odors	orientation to food plant	amputation	Deseö (1976)
Trichoplusia ni Hübner	flower odors	orientation to flowers	EAG	Grant (1971)
<i>Orthoptera</i> (larvae & imagines) Acrididae (Locusta)	grass odor	orientation to plants:	amputation	Kennedy & Moorhouse (1969)
	hexenal, hexenol	anemotaxis	s. basiconica	Boeckh (1967, 1974)
	fatty acids		s. coeloconica	Kafka (1970) Kafka et al. (1973)
	oxygenated org. compounds nitrogenated compounds		s. coeloconica	
<i>Hemiptera</i> Brevicoryne brassicae L.	host plant odor, sinigrin	orientation to host plants	amputation	Pettersson (1973)
	host plant extracts	orientation to host plants	EAG	Pantle & Feir (1976)
	repellent	walking	amputation	Feir & Beck (1973)
Planococcus citri Risso			amputation	Salama (1971)

Trioza erytreae Del Guercio	host & nonhost plant odors	walking & probing	amputation	Moran & Brown (1973)
<i>Maxillary palpi of imagines</i>				
<i>Diptera</i>				
Calliphora vicina Robineau-Desvoidy	flower odor compounds: same as for antennae	orientation to food?	El.phys.: s. basiconica	van der Starre & Tempelaar (1976)
blowflies	repellents		amputation	cf. Dethier (1963)
<i>Antenna of larvae</i>				
<i>Coleoptera</i>				
Leptinotarsa decemlineata Say	host plant odors	orientation to plant biting	amputation	Chin (1950)
Otiorrhynchus sulcatus	CO ₂	orientation to plant roots	amputation	Klingler (1966)
<i>Lepidoptera</i>				
different sp.	plant odor compounds	orientation & biting	amputation	Dethier (1941)
Bombyx mori L.	hexanol, hexenol, butylaldehyde	?	El.phys.: s. basiconica	Morita & Yamashita (1961)
	plant odor compounds	orientation, feeding	amputation	Ishikawa et al. (1969)
different sp.	plant odor compounds	orientation & biting	El.phys.: diff. sensilla	Schoonhoven & Dethier (1966) Dethier & Schoonhoven (1969) Dethier (1976)
Manduca sexta Johanssen	plant odor compounds	feeding, host selection	amputation	Hanson & Dethier (1973)
<i>Maxillar sensilla styloconica of larvae</i>				
<i>Lepidoptera</i>				
Manduca sexta Johanssen	odors of macerated plant	feeding	El.phys.: lateral s. styloconica	Staedler & Hanson (1976)

ERRATA

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page p = paragraph ln = line

- 26 Jeffrey K. Waage was in attendance.
- 29 2nd photo caption, 2nd line, "H.J. McCracken" should read "R.J. McCracken"
- 72 p 3, ln 5, add "s" to "freshwater"
- 74 ln 2, after "reduce" add "tidal movements of air in and out of the spiracles and so reduce"; p 1, ln 10, "vanderplankei" should read "vanderplanki"
- 75 Fig. 2, after "Hinton" add "after immersion in tap water following a 10-year period"
- 76 p 2, ln 9, "acdysis" should read "ecdysis"
- 77 p 1, ln 5, "bettle" should read "beetle"
- 78 & 79 transpose
- 80 ln 8, "*Zenilla*" should read "*Zenillia*"; 4th ln from bottom, "Pthiraptera" should read "Phthiraptera"
- 81 p 1, ln 9, delete "though"; Fig. 6, between "the" and "trochanter" add "indirect flight muscles and the tergal depressor of the"
- 82 Anderson, 1972b, after "Vol. 1" add "pp. 165-242"; "Clark" should read "Clarke"; "Deegner" should read "Deegener"; Hinton, 1976, move "pp. 43-78" to follow "Cheng"; Lubbock, J., "1974" should read "1874"
- 212 p 1, ln 1, "interractions" should read "interactions"; p 2, ln 7, "events" should read "insects"; Fig. 1, "theyr" should read "their"
- 213 p 1, ln 5, "abscre" should read "obscure"; p 4, ln 6, "insects" should read "events"
- 222 p 1, ln 10, "exretory" should read "excretory"; p 4, ln 9, "classified" should read "classical"
- 224 p 3, ln 1, "conceputal" should read "conceptual"; ln 6, "interractions" should read "interactions"; ln 8, "derive" should read "derives"; ln 10, "derives" should read "derive"; p 4, ln 8, "curcial" should read "crucial"; p 5, ln 7, "ehcmical" should read "chemical"
- 554 p 1, ln 11, " Mx_n " should read " $Mx_n(\cdot)$ "; " $lx_{n-1}0$ " should read " $lx_{n-1}0$ "; p 2, ln 5, "(St)" and "(Rt)" should read "(S)" and "(R)"; formula (3), delete all "t" after "S"
- 555 formula (4), delete all "t" after "R"; ln 4, delete "t" after "S" and "R"; formula (7), "F" should be inside parenthesis; formula (8), delete "t" after "R", "s" should read "S"; "M" should read "M̄"; formula (9), delete "t" after "S" and "R"; ln 2 after form. (9), delete "t" after "S" and "R"; ln 5 after form. (9), " $\frac{dp}{dt}$ " should read " $\frac{dp}{dt}$ ", delete "t" after "S" and "R"
- 556 ln 2, delete "t" after "S" and "R"; ln 4, "fruit" should read "fruits"; ln 5, "all" should read "and"
- 557 ln 1 after formula (10), "requirement" should read "requirements"; p 3, ln 2, "or" should read "of"; ln 7, "depicts" should read "depict"
- 558 p 1, ln 6, "(In Press)" should read "(1976)"; DeMichele, "(In Press)" should read "(1976)", after "Ent." add "5: 1011-16"
- 560 p 2, ln 7, delete "examples of"; ln 8, delete "which"
- 561 p 5, ln 2, "explicitlyly" should read "explicitly"
- 562 p 2, ln 1, delete "and"; p 3, ln 6, add "permitting" after "conditions"; p 4, ln 1, "effective" should read "effect of"; ln 2, delete "effect of"
- 563 p 2, ln 5, delete "," after "1972)" add "."
- 564 p 7, ln 2, "cuased" should read "caused"
- 565 p 5, ln 4 should read "response to changes in host density and their own density. In general, these"
- 567 p 2, ln 8, add ";" after "(K)"
- 568 ln 2, delete "(dt)"; p 2, ln 3, "predators" should read "prey"; p 3, last ln, "randon" should read "random"
- 570 p 2, ln 11, "of" should read "for"
- 571 ln 3, add "or" after "territoriality"
- 573 formula (8), " N_1 " should read " N_A "
- 574 last ln, add "," after "random"
- 575 p 3, ln 7 from bottom, delete "theory, though readily"; ln 6 from bottom, delete "This fragmentation though phase of a cycle each is in, the population as a whole would persist."; ln 5 from bottom, "though" should read "although"
- 576 p 2, last sentence, delete ", one"
- 577 formula (15), " H_a " should read " H_a "

$$\frac{P_t}{P_t}$$
- 578 p 2, last ln, "(3)" should read "(2)"; next-to-last ln, "is that" should read "are that"; p 4, last ln should read "Finally, Auslander et al. (1974), using a differential equation model, indicated that an interaction in which the parasite attacks, or prefers, a particular age class of its host may provide stability to such an interaction."
- 580 ln 3 from bottom, "permiteed" should read "permitted"

- 581 p 2, add after ln 2 “to that of the target pest; (3) the bionomics of the pest species in both areas; (4) the natural enemy fauna associated with the host in the target area; and (5) the parasitic habit of the proposed entomophagous species; e.g., whether it is a primary or secondary parasite or a cleptoparasite. Further, the pre-introduction studies should also determine whether the parasite is effective at low host”
- 582 ln 13 from bottom, “ncecessary” should read “necessary”; p 3, ln 2, “footstuff” should read “foodstuff”
- 583 p 3, ln 6, add “including habitat” after “processes”; p 1, ln 3, delete “of” after “capabilities”, insert “and”
- 584 Hassell, 1969, ln 2, add “38: 329-339.”
- 585 Nicholson, A.J., “1973” should read “1933”; after Nicholson, 1935 add reference “Parker, F.D. 1971. Management of pest populations by manipulating densities of both hosts and parasites through periodic releases. *In* C.B. Huffaker (ed.). Biological Control. Plenum Press, New York, pp. 365-376.”; “Rodgers” should read “Rogers”
- 586 add after Ulyett, 1947 reference “1950. Distribution of Progeny by *Cryptus inornatus* Pratt (Hymenoptera: Ichneumonidae). Can. Entomol. 82: 1-11.”; Zwolfer, last ln, delete “Pp. 189-207.”
- 719 p 1, ln 3, “mutagensis” should read “mutagenesis”; p 3, ln 4, add “uncertainty of human epidemiologic data necessitates” after “and”
- 720 p 5, ln 2, add “in paragraph” after “(1)”; p 9, ln 3 & 4, delete commas before and after “and Hayes (3)”
- 721 p 4, ln 4, delete “,” after “carcinogens”; p 6, ln 3, “energy” should read “energy”; ln 5, add after “cancer” “would be expected to occur, in the exposed population, during an entire lifetime. In considering carcinogenic risk assessment let us refer to the EPA posture on the matter.

As the Administrator of EPA, Mr. Train stated recently: ‘It is extremely important that the leading government agencies work closely with each other and with experts outside the government in the field of carcinogenicity in the development of government procedures and policies concerning cancer. I am publishing (these) interim procedures and the guidelines in the Federal Register not only to provide public notice of the approach which EPA will be following in our current activities but also to stimulate commentary from all sources upon that approach . . . I also plan to meet personally with leading authorities in this area as part of a continuing process to discuss these cancer policies and exchange information and views.’

The preliminary guideline for Carcinogen Risk Assessment, as outlined by the EPA, describes a framework to be followed in analyzing carcinogenic risk. Some salient principles to be used in evaluating the quality of data and formulating judgments concerning the nature and magnitude of the cancer hazard from suspect carcinogens are discussed.

The recommended guidelines are within the policy framework and legislation already in existence. No one specific kind of data is deemed prerequisite for regulatory action to control, prohibit, or accept a carcinogen. Let me summarize the major points and philosophy expressed in these interim procedures.

The analysis of health risks will be carried out independently from the socio-economic consequences of regulatory action. The central purpose of the Health Risk Assessment will be to provide a judgment concerning the weight of evidence that an agent is a”; last p, ln 6, add “-” after “nonlife”

- 722 p 2, ln 3, “epidemiology” should read “epidemiological”; p 6, ln 2, delete “Other published critiques whether supportive human carcinogenic potential.”; ln 5, “longterm” should read “long-term”; last p, ln 4, “undertainties” should read “uncertainties”
- 723 p 3, last ln, add “(9)” after “range”; p 4, ln 3, “extrapolating” should read “extrapolation”; ln 6, add “generally” after “one-hit” and “probit”; Fig. 1, “Slope 264” should read “Slope 2.64”; “(1/1000,000,000)” should read “(1/100,000,000)”
- 724 p 3, ln 2, delete “was”
- 725 Table II, “long” should read “log”; “1/130” should read “1/135”; p 1, ln 9, delete “100” add “a”
- 726 p 3, ln 3, “10⁻⁶” should read “10⁻¹⁴”; p 4, ln 4, transpose “previously mentioned” and “(1)”; last p, last ln, “science” should read “significance”
- 727 p 4, ln 1, “new borns” should read “newborns”; p 5, ln 4, “dysmorphology” should read “dysmorphologic”; p 6, ln 3, delete “to” after “exposures” add “of”; p 7, ln 9, delete “the” after “on”
- 728 p 2, ln 1, add “and industrial chemical” after “fungicide”; ln 3, add “industrially discharged” before “mercury”; p 3, ln 3, add “my” after “briefly”; last p, ln 4, “afriad” should read “afraid”
- 729 p 2, ln 5, add “(” after “assumptions” and “)” after problem”; Table V, 0.05 + 12.50 = “12.50” should read “12.55”; last p, ln 4, add “,” after “continued” and “at” after “reached”
- 730 p 7, ln 4, delete “,” after “Carter”; ln 6, “contaiminated” should read “contaminated”; p 9, ln 2, “2,4,5T” should read “2,4,5-T”; no new p at “Simply”; ln 5, “2,4,5T” should read “2,4,5-T”; ln 7, “halflife” should read “half-life”
- 731 1st formula, “2,2,4,5-T” should read “2,4,5-T”; “there is 10,000 times less” should read “there is 10,000,000”; p 2, last ln, delete “the” after “of”, “mutagenesist” should read “mutagenesis”; p 4, ln 4, add “progeny” after “original”; ln 5, delete “before”, add “to”, add “before it” after “generation”; p 6, ln 2, “closed” should read “close”
- 732 p 1, ln 3, “mutagent” should read “mutagen”; p 5, ln 1, “reflect” should read “reflects”, “mutation” should read “mutational”
- 733 p 2, ln 6, “system” should read “systems”
- 735 Gehring, ln 2, “2,5,5-” should read “2,4,5-”; Crow, ln 1, “Dilema” should read “Dilemma”, “Mulations” should read “Mutations”; Vogel, add “1970” after “Rohrborn”; Obe, ln 2, “Drosphila” should read “Drosophila”

ADDITIONS

- 9 after Francisco Ayala, add Baccio M. Baccetti Italy
31 (opening remarks by Dr. Anastos)

Before making the announcements, acknowledgments are due to those who have been involved in organizing this XV International Congress of Entomology.

From the time the United States of America was designated as host for the Congress, many people and organizations have graciously lent their talents and have given generously of their time to assure the success of the Congress.

With so many involved, it obviously is impossible to recognize all of them individually at this time. However, all of them are acknowledged in the Program of the Congress.

Nonetheless, I do wish to acknowledge a select few for their outstanding service to the Congress. These individuals are: Mr. Gerald Odland and Miss Barbara Waite of my staff; The Entomological Society of America and its Executive Director, Dr. Wallace P. Murdoch, as well as the entire headquarters staff of the Entomological Society of America; Dr. John V. Osmun and Dr. Ernest C. Bay who preceded me as Secretary-General; the staff of the Washington Hilton Hotel and in particular Mr. Gene F. Razzante and Mr. Werner Lewin, Jr.; and finally, one individual who has carried the brunt of the planning and organizing of the Congress during the past four years and to whom we all owe a great debt of gratitude, the President of the Congress, Dr. Curtis W. Sabrosky. A round of applause is in order for all of these named, as well as the unnamed individuals and organizations. (Applause)

- 33 (closing remarks, Dr. Anastos)

An announcement concerning the registration figures for the Congress.

The number of registrants in attendance	2,350
The number of preregistrants that did not attend	166
The total registration of the Congress	2,516
Total number of countries represented by the Congress	73

The XV Congress is now approaching its end and soon it will belong to history. For those of us who have had the privilege of serving as hosts, we hope your stay was a memorable experience. We enjoyed serving you and hope to see you again. On behalf of the Secretariat, we wish you a fond farewell and a safe journey home.

Maxillar and labial palpi of larvae

Coleoptera

Leptinotarsa decemlineata Say	host plant odors	orientation to plant, biting	amputation	Chin (1950)
Otiorrhynchus sulcatus F.	CO ₂	orientation to plant roots	amputation	Doane & Klingler (1966)
Ctenicera destructor Brown	CO ₂	orientation to plant roots	amputation	Doane & Klingler
Agriotes spp.	CO ₂	orientation to plant roots	amputation	(in prep.)
Orthosoma brunneum Forster	CO ₂	orientation to plant roots	amputation	Meeking et al. (1974)

Lepidoptera

Bombyx mori L.	host plant odors	orientation, feeding	amputation	Ishikawa et al. (1969)
different sp.	host plant odors	orientation, feeding	El.phys.: s. basiconica	Schoonhoven & Dethier (1966)

have also been found on the ovipositor of flies (Wallis 1962, Hooper et al. 1972). A possible role in phytophagous insects seems likely but has not yet been studied.

In Table 1 an attempt has been made to summarize reports on olfactory sensilla involved in insect plant interactions. The older literature on chemoreception of insects has been reviewed with much expertise by Dethier (1963) and Schoonhoven (1968). Our knowledge of chemoreceptive sensilla sensitive to plant compounds is still scarce. This is not only due to the limited number and scope of investigations but also to the lack of knowledge of plant chemistry.

In most insects plant odors can release orientation (for references see Table) to the source, however, frequently this is only detectable over very short distances. Other activities might be influenced as well such as walking and probing in Homopteras, and stimulation of oviposition and oögenesis in moths.

Nectar and pollen feeding insects can get attracted not only by specific colors and patterns but also by different odors of flowers. The olfactory sensilla of blowflies (*Sensilla basiconica* in antennal pits), of bees (*S. placodea*), and butterflies (*S. basiconica*) do indeed have "flower odor" receptor cells. In the fly *Calliphora*, the bee, and the *Antheraea* butterfly different receptor cells were found to have reaction spectra including compounds belonging to derivatives of aliphatic hydrocarbons, aromatic hydrocarbons, bicyclic terpenes and macrocyclic compounds.

Different pest insects associated with cruciferous crop plants have long been known to be attracted by the mustard oil glucoside sinigrin and its aglycon allylisothiocyanate (Verschaffelt 1910, Goernitz 1957, for further references see Schoonhoven 1972b). Recently the stimulation of the antennal sensilla of the cabbage root fly by isothiocyanates has been reported. Apparently the cabbage aphid can also detect both sinigrin and the aglycon with its antennae.

Different insect larvae living in the soil and in decaying wood have proven to be responsive to CO₂. Both ecological habitats have an elevated CO₂ content and in addition roots have proven to produce a CO₂ gradient used by different root feeding larva for orientation. From amputation experiments the conclusion has been drawn that the sensitive sensilla are located on the maxillary- and labial palpi, and possibly also on the antenna. Since CO₂ perception seems to occur in very different insects (even aphids, Pettersson 1973) it would be interesting to compare the receptors cells of soil living insect with other insects like bees (Lacher 1964, Stange and Diesendorf, Stange 1975) and animal parasites (see Galun this vol.).

Sensilla with similar sensitivities for insects with common host plants: coniferous trees have been described for bark beetles, the spruce budworm, a siricid wasp, and the pine weevil. The last species is unique in the sense that it has an antennal receptor cell with a narrow specificity (reaction spectrum) for the typical and prominent host terpenes: α - and β -pinene and camphen. Such high specificity has only been reported so far from pheromone receptor cells (cf. Payne 1974). Other receptor cells studied also in detail (e.g., Acrididae, Diptera, Lepidoptera) have been found to have much larger reaction spectra.

Finally the study of Staedler and Hanson (1975) should be mentioned which questions our distinction between olfactory and gustatory sensilla. The investigated lateral *Sensillum styloconicum*, a typical taste organ with a tip porus, was found to respond to the odor of a cut host leaf. The question arises if this close range olfactory capability is a common, so far undetected feature of all gustatory sensilla (see also Dethier 1972). Probably not, since the medial *S. styloconicum* did not respond to the same olfactory stimulation. However, future studies of contact chemoreceptive sensilla should consider odorous as well as nonpolar compounds as possible stimuli.

(C) Contact Chemoreception

The distribution, morphology, and general physiology of contact chemoreceptive sensilla in general are given by Dethier (1963), Sinoir (1969a), Slifer (1970), Stuerckow (1970), and Hodgson (1974). The sensilla are most numerous on the mouth-parts and the tarsi. Reports on gustatory receptors in antennal sensilla are limited. The first electrophysiological study of such sensilla on the antenna of the cockroach has been published recently (Rueth 1976). Reports on contact chemoreceptive sensilla on the antenna involved in insect plant interactions are scarce and based only on behavior observations (Schoonhoven 1966, Pflumm 1972).

Table 2 gives some compiled information on the function of contact chemoreceptive sensilla responsible for the perception of host plant stimuli. In gustatory sensilla several receptor cells with similar though not identical spectra of sensitivity can be found. In his comparative review

Table 2.—Perception of plant stimuli by contact chemoreceptors

Same abbreviations as in table 1.

Species	Perceived stimuli	Released behavior response	Investigation	References
<i>Galea (Maxilla) of imagines</i>				
<i>Lepidoptera</i> (Proboscis) Choristoneura fumiferana Clem.	sugars	feeding	El.phys.: s. styloconica	Staedler & Seabrook (1975)
<i>Maxillar and labial palpi of imagines</i>				
<i>Orthoptera</i> (larvae & imagines) Acrididae (locusta, Schistocerca)	sugars, salts, acids, aminoacids, diff. deterrents, grass extracts	feeding	amputation & ablation El.phys.: peg sensilla	Haskell & Mordue (1969) Sinoir (1969b) Louveauux (1976) Haskell & Schoonhoven (1969) Blaney (1974, 1975)
<i>Labium of imagines</i>				
<i>Diptera</i> (Proboscis) Blowflies	H ₂ O, salts, sugars, acids, amino acids, fatty acids, glucosides, alcohols different foods vapors of nonpolar compounds salts, sugars salts, sugars	feeding deterrence feeding, deterrence feeding, deterrence	El.phys.: s. chaetica El.phys.: taste papillae El.phys.: s. chaetica	reviews: Dethier (1974a) Kijama (1976) Hansen et al. (1976) Dethier & Hanson (1965) Dethier (1963, 1972)
<i>Ceratitis capitata</i> Wied. <i>Drosophila melanogaster</i> Meig. <i>Psila rosae</i> F.	 sugars	 	El.phys.: s. chaetica El.phys.: s. chaetica El.phys.: s. chaetica	Gothliff et al. (1971) Isomo & Kikuchi (1974) Falk & Atidia (1975) Staedler (1976)

<i>Heteroptera</i> Dysdercus sp.	sugars	feeding	El.phys.: hair sensilla	Bresch (1973) cit. Wieczorek (1976)
<i>Epipharynx (Clypeo-labrum) of imagines</i>				
<i>Orthoptera</i> Acrididae (Locusta & Schistocerca)	same compounds as palpi	feeding	El.phys.: small papillae ablation	Haskell & Schoonhoven (1969) Louveau (1976)
<i>Tarsi of imagines</i>				
<i>Diptera</i> Blowflies (Phormia calliphora)	H ₂ O sugars, salts, acids vapors of nonpolar compounds	feeding	El.phys.: s. chaetica	reviews: McCutchan 1969 Van der Starre 1972 Dethier (1972) Shiraishi & Tanabe (1974) Pietra et al. (1976)
Psila rosae F.	sucrose	feeding	El.phys.: s. chaetica	Staedler (1976)
<i>Coleoptera</i> Chrysomela brunsvicensis Gr.	H ₂ O, salt, hypericin	feeding, host selection	El.phys.: s. chaetica	Rees (1969)
Leptinotarsa decemlineata Say	salt, sugar? alkaloid- glucosides	feeding, host selection	El.phys.: s. chaetica	Stuerckow (1959)
<i>Lepidoptera</i> Vanessa indica L. Danaus gilippus berenice Cramer Pieris brassicae L.	salt, sugar host plant H ₂ O, salt, mustard oil glucosides	feeding host selection: oviposition oviposition	El.phys.: s. chaetica ablation El.phys.: s. chaetica	Takeda (1961) Myers (1969) Ma & Schoonhoven (1973)

Maxilla (galea) of larvae: Sensilla styloconica

<i>Coleoptera</i> Leptinotarsa decemlineata Say	salt, sucrose, amino acids, chlorgenic acid	feeding	El. phys.	Mitchell & Schoonhoven (1974) Mitchell (1974)
<i>Lepidoptera</i> different sp.	salt, sugars; inositol, aminoacids, various deterrents, plant extracts		El. phys. amputation	reviews: Schoonhoven (1969a, 1972c) Dethier & Kuch (1971) Dethier (1973) Ishikawa et al. (1969)
Manduca sexta Johanssen	plants	feeding, host preference	amputation	Hanson & Dethier (1973),
Spodoptera exemota Wilk.	plants	feeding, host preference	amputation	Ma (1976)
Pieris brassicae L.	mustard oil glucosides	feeding	El.phys.	Schoonhoven (1967b) Ma (1976)
Mamestra brassicae L.	mustard oil glucosides	feeding	El.phys.	Wieczorek (1976)
<i>Maxillar and labial palpi of larvae</i>				
<i>Coleoptera</i> Leptinotarsa decemlineata Say	salts, sugars, amino acids	feeding	El.phys.: palp tip	Mitchell & Schoonhoven (1974)
<i>Lepidoptera</i> different sp.	salts, sugars	feeding	El.phys.: s. basiconica	Schoonhoven & Dethier (1966)
Manduca sexta Johanssen	plants	feeding, host preference	amputation	Hanson & Dethier (1973)
<i>Epipharynx of larvae</i>				
<i>Lepidoptera</i> Pieris brassicae L.	salts, sugars, alkaloids, steroids	feeding, swallowing	El.phys.: small papilla	Ma (1972)

Schoonhoven (1974b) and Dethier (1973, 1974a) mentioned the following receptors: water, sugars, cyclotols, aminoacids, glucosides, acids, vapours of some non polar compounds and "bitter" substances (deterrents). Since the corresponding stimuli probably do occur in most, if not all plant parts and its products the occurrence of these receptor cells seems to be of selective value. Numerous behavior and electrophysiological studies prove that the perception of the mentioned compounds are most important for feeding in general and for host selection in particular. Insect deterrents such as alkaloids and steroids are widely distributed in plants and have been shown to be of particular importance since their botanical distribution can decisively determine the host plant spectrum of phytophagous insects (Jermy 1966, Levinson 1976, Schoonhoven and Jermy 1976).

Special attention has been focused on contact chemoreceptive sensilla of Lepidoptera larva: the maxillary sensilla styloconica. These two pairs of sensillar are important for host selection and induction of feeding preferences (Hanson and Dethier 1973, Ma 1976). Since these sensilla have only 2 sets of 8 equal or similar receptor cells their physiological responses should be more easily correlated to the behavior (feeding choices) than in other insects such as the blow fly having in the average a total of 125 hairs and 66 papilla sensilla with each up to four chemoreceptive cells. Indeed Ma (1972) could show such qualitative and quantitative relations successfully giving fairly good correlations between the feeding response of *Pieris brassicae* L. and either the activity of the sugar receptor (stimulating) in the lateral sensillum, and the epipharynx sensillum or the activity in alkaloid sensitive receptor (inhibitory) of the medial sensillum.

In *Pieris brassicae* L. and *Mamestra brassicae* L., both feeding on Cruciferae, receptor cells have been identified sensitive to the mustard oil glucoside sinigrin. At this point it has to be referred again to the already mentioned olfactory sensilla of Cruciferae associated insects which perceive the aglycon of sinigrin. Interestingly sinigrin alone is not feeding stimulatory for *Pieris*. However, Ma (1972) could show a synergistic effect between the glucoside (and other compounds) and sub-optimal concentrations of sucrose.

It is a well established fact that insects have contact chemoreceptive sensilla on their tarsi. In different flies and the butterfly *Vanessa indica* L., they are apparently involved in the search of food and contain cells sensitive to similar compounds as the proboscis chemoreceptors. In all the other investigated tarsal setae no or only weak responses to stimulation with sucrose has been observed. But instead chemoreceptive cells have been identified which are sensitive to specific host plant compounds such as sinigrin (*Pieris*), hypericin (*Chrysomela*) and specific alkaloid glucosides (*Leptinotarsa* adults). In the first two examples the receptors for the "host plant sign stimuli" mediate oviposition and feeding. The Solanaceae alkaloids are deterrents for *Leptinotarsa* but interestingly the alkaloid glucoside solanine occurring in the host plant (potatoe) has a ten times higher stimulation threshold than the other tested compounds (Stuerckow 1959). It is suggestive that tarsal chemoreceptors may be specially adapted to the perception of "host plant sign stimuli."

At this point the question arises how the tarsal chemoreceptors can perceive chemical stimuli which are non-sapid, non-polar and seem to occur in the surface waxes. The same problem exists for the peg-like sensilla on the dome of the maxillary palps of Acridids. Grasshoppers discriminate between acceptable and unacceptable food plants during palpation of the still undamaged leaf surface (Blaney and Chapman 1970). Blaney (1975) has shown that the involved chemoreceptors can be stimulated by leaf waxes which mediate the necessary information for host selection (Bernays et al. 1976). Staedler (1976) could prove that the surface waxes of undamaged carrot leaves do contain compounds (not waxes) stimulating oviposition in the carrot rust fly. The corresponding receptors have not yet been identified, but olfactory sensilla on the antenna and palpi are not essential for perception.

Further evidence for the perception of leaf-surface compounds has been accumulated by behavioral studies of aphids (Klingauf et al. 1971, Klingauf 1972). The authors isolated from the leaf-surface of *Vicia faba* L. an n-paraffin ($C_{32}H_{66}$) influencing the duration of the first probing of the aphid *Acyrtosiphon pisum* (Harris). In addition, Klingauf (1971) also reported that phlorizin a typical glucoside of Pomoideae isolated also from the leaf surface does influence both first walk and probe on a non-sapid inert substrate. The sensitive sensilla have not yet been identified.

Discussing the perception of leaf-surface chemicals Bernays et al. (1975) suggested that the extra cellular fluid bathing dendrites (first described as viscous fluid on the sensillum tip by Stuerckow 1967) is involved and may be responsible even for some of the specificity of chemoreceptive cells. Since contact chemoreceptive sensilla can have a limited olfactory capability (Staedler and Hanson 1975), it might be that the transport mechanism of absorbed stimuli to the receptor membrane of the

“gustatory” sensilla is similar as it is conceived by Kaissling (1974b) and Steinbrecht (1974b) for olfactory receptor cells.

Sensory Codes for Plant Perception

This is the central question of any study of sensory aspects of insect plant interactions. Namely, how do the sensory neurons transmit the sensory information perceived to the CNS (central nervous system). This process interests not only entomologists mainly concerned with the behavior output of pest insects: “destruction of crop plants,” but also biologists devoted only to basic research.

How can we “break the code”? For long the only approach was to study the qualitative and quantitative correlations between the response of the sensory receptor cells and the behavior. In recent years attempts were made to correlate the sensory activity (olfactory receptors) not only with the output of the central nervous system: behavior, but also with responses of central interneurons which presumably encode the sensory information. Yamada (1971b), Masson and Strambi (1975), Suzuki (1975) and Boeckh (1976) reported on their results and gave reviews of this new area of investigation.

In insect olfaction the necessity and hypothetical function of olfactory coding has been recognized early by Schneider et al. (1964). The principles have been recently explained and documented with much expertise by Yamada (1971b), Boeckh (1974, 1976) and Boeckh et al. (1975). As a result of the detection of the broad reaction spectra of gustatory receptor cells Dethier (1973, 1974a) and Blaney (1974) developed the concept of coding also for the contact chemoreceptors.

Basically two different encoding mechanisms could be assumed. First we can think of a system giving just yes or no outputs in response to receptor cells mediating acceptance (e.g., sugar, host plant “sign” stimulus) or rejection (e.g., salt, deterrents, repellents). This was the earlier concept as it appeared from the first electrophysiological studies of the blowfly (cf. Dethier 1974a). The second system is much more likely to describe the reality assuming a broader analytical capacity of the hypothetical encoding mechanism in the CNS. Indeed behavior reactions are usually not only bimodal (yes or no reaction) but show more differentiated or graded responses. The more complex code required could be achieved by the concept of across fiber patterning. This principle has been described and explained in detail by Dethier (1973, 1974a). In short, using the words of Dethier (1974a), such a potential for discrimination among many substances can be realized as follows: “The CNS does not merely determine whether ‘acceptance’ input dominates ‘rejection’ input, or vice versa, but assesses instead in a qualitative fashion the input from all types of receptors. It is proposed in other words that the total pattern, or Gestalt, is the significant parameter” Coding with across fiber patterns can be performed by chemoreceptor specialists with discrete, now overlapping reaction spectra or by groups of receptors with overlapping spectra. Both mechanisms seem to exist as already discussed. Broader reaction spectra seem to be more abundant and have, according to Boeckh (1976), the following advantage over narrow “specialist” receptors: since discrimination is provided by the generation of a great number of different substance specific impulse patterns, a higher number of receptor cells of fewer reaction types can be involved in chemoreception. This gives a higher density of “receivers” which results in a higher sensitivity.

A total pattern, relating to the idea of “Gestalt” perception, should be thought of generated not only by some populations of chemoreceptors but by many sensory receptors of different modalities and organs. Dethier (1973, 1976) stressed this point when discussing the host selection of Lepidoptera larva. Further compelling evidence exists that across fiber patterning, together, with a corresponding central decoding, plays a major role in chemoreception involved in insect plant interactions. Such examples include blowflies (van der Starre 1972, Dethier 1974, Pietra et al. 1976), the locust (Blaney 1975) and the honey bee (Vareschi 1971). Interestingly in sex pheromones perception where highly specialised receptor cells have been described (cf. Payne 1974) the perception of individual components of the attractants seem to involve also across fiber patterning (O’Connell 1975).

The mentioned recordings from the central nervous system provide the first direct evidence for central encoding processes. Boeckh (1974, 1976) and his coworkers Boeck et al. (1976), Suzuki (1975, and Suzuki et al. (1976) have been able to identify the following elements: (1) spatial convergence of inputs from olfactory receptors of all regions and of both antenna; (2) convergence from receptor cells of different stimulus modalities and qualities (e.g., mechano-, chemo-,

thermoreceptors). The identified central neurons have shown to be less specific to pure compounds and, most remarkably in the context of host selection, very specific for complex odors like fruits which stimulate many primary receptor cells.

These exciting results and the developed concept of across fiber patterning may give the impression that the main problems of insect chemoreception have been solved. However, the prominent difficulty of recording from chemosensory neurons is their variability. This can be so dominant that it is impossible to analyze the recordings in terms of a sensory code. The problem of variability has been discussed recently by several authors underlining its importance: Van der Starre (1972), Dethier (1974b), Blaney (1974, 1975), Schoonhoven (1976). Possible and proven factors of this variability can be the following: (1) controllable variance due to the age of animals, feeding history, humoral effects, synergistic and inhibitory actions on the receptor level, and recording artefacts; (2) differences between animals, sensilla and chemoreceptive cells, and repetitions (time).

If recognized the first group of factors can be controlled. As in *Manduca sexta* Johanssen, prior feeding experience can have proven effects on the sensitivity of chemoreceptive cells (Schoonhoven 1969b, Ma 1972, Staedler and Hanson 1976). The effect of humoral factors on the palp sensilla of the locust have been described by Bernays and Chapman (1972), Bernays et al. (1972) and Bernays and Mordue-Luntz (1973). An interesting artefact: the ion depletion of gustatory sensilla by deionized water has been discovered recently by Broyles et al. (1976).

The second group of factors can not be influenced. The CNS is of course also "confronted" with the "noise" of receptor cells. Probably interneurons at successively higher levels of the CNS can "smooth" this noise. In order to cope with the variance the investigator should design both behavior and electrophysiological experiments so as to allow a proper statistical analysis (cf. Blaney 1975). This means that to provide the basis for a better replicability of our results we have to identify the different sources of variance (cf. Schoonhoven 1976). This is especially important if "natural" chemical stimuli are applied. Such extracts or entire plant parts are more likely to produce complex responses in the stimulated cells of a sensillum than pure chemicals.

In this context attention should also be drawn to the problem of identification of individual receptor cells. This obviously is most important if a sensory code and its variability is investigated. Different techniques have been applied and discussed (cf. Schoonhoven and Dethier 1966, Vareschi 1971). All have in common that the chemical composition of the adequate natural stimuli should be known which only allows the identification of the reaction spectrum of individual receptor cells. It is therefore clear that our lack of knowledge and the difficulty to obtain sufficiently pure chemicals can often be the main obstacle for progress in the study of chemoreceptors involved in plant insect interactions.

In the view of present results it can be said that several requirements should ideally be met allowing a successful investigation of sensory coding. This points to the fact that sensory physiology alone will not be able to "crack a sensory code." Sensory aspects of insect plant relationships can only be elucidated using an interdisciplinary approach based on behavior studies and chemical analysis of host plant stimuli. Such investigations will advance not only our understanding of the biology of sensory physiology but may eventually lead to necessary improvements in pest control.

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The Effect of Plant Secondary Products on Insect Plant Co-evolution

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ABSTRACT

It is generally agreed that the chemistry of all plants in any habitat by and large determines the richness or otherwise of insect life. However, the various chemical strategies that a plant species displays have been determined by evolutionary forces, and are geared to deter not only insects but all other potential 'predators' from bacteria to man. Obviously, the metabolic requirements for defense cannot be allowed to mount so high that the plant has no energy budget to expend on reproduction. So different families of plants have selected from the chemical armoury available and concentrated on two or three main components to accumulate. The role of evolution in that choice is discussed.

It can be taken as axiomatic that in any given ecosystem the fates of the various guilds of herbivorous insects and plants are chemically intertwined (Gilbert and Raven 1975, Swain 1976b, Van Emden 1973). This does not mean that all the interactions observed depend on chemical factors; in some cases the gross morphology of both insects and plants and the influence of pathogens, and predators and other herbivores are of equal significance. Nevertheless, herbivorous insects are totally dependent on the nutritional status of the plants on which they feed and the balance between the amounts of sterols, sugars, necessary amino acids and other required co-factors on the one hand and that of actual or potential toxins on the other must have a profound effect on the insects' well-being. The selection of a particular, or many, species of plant by a given insect as a source of food either for itself or its progeny is obviously of enormous importance in determining its evolutionary success. Although, in general, one can regard certain organs of all plants (especially young leaves and stems, mature fruits and seeds), as being potentially nutritious to every insect, their selection of plants as foods is, as we know, highly specific (Schoonhoven 1972, Kogan 1976, Städler 1976). This has led to the idea that it is the quality and quantity of potential toxins which determines the selection of specific plant foods by any single insect species (Dethier 1970, Feeny 1975, Janzen 1975, Van Emden 1973). It is generally agreed that most toxins are secondary plant products (Table 1) and that the few species of insect which can successfully utilize a given plant either for food or for ovipositing, do so by having evolved suitable detoxification systems which can overcome these chemical defences, the very mixture of compounds which deters the many guilds of other sympatric insects. But it is known that in natural ecosystems, the selection by an insect of an individual plant is dependent on its abundance and that of other species of plants in the vicinity (Alsatt and O'Dowd 1976). For example, the Colorado beetle, is more attracted to *Solanum nigrum* for ovipositing than it is to its true host, the common potato *S. tuberosum*, although the former is almost completely lethal to the developing larvae. It follows that it is the chemistry of all plants in any given habitat which by and large determines the richness or otherwise of insect life.

We must remember, however, that there may well be gross differences in the acceptability of plants to insects as food depending on their mode of feeding, and on their ability to excrete, sequester or detoxify (Feeny 1975) potentially harmful compounds. For example, aphids and other hemipterous phloem-sucking insects generally may not have to deal with plant toxins in high concentration, except insofar as these act as feeding signals, since many, but not all, such compounds are usually entirely absent from plant sap or occur there in much lower concentrations than in the

organs in which they are normally found (Van Emden 1976). Other insect species, notably diptera, browse externally on the surface of plants (Southwood 1973) and, therefore, again most probably do not come into contact with the whole range of defensive substances which the plant produces. Finally, the nectar and pollen collecting insects are undoubtedly attracted by primary biochemical nutrients and encounter few toxins (Baker and Baker 1975).

It is not possible in the space available to describe fully the complexity of chemical defences which plants possess against insects, other herbivores and phytopathogens, but these have been well reviewed elsewhere (Swain 1976b, Gilbert and Raven 1975, Städler 1976, Schoonhoven 1972, 1973). Instead, I will concentrate on one important aspect, namely the evolution of secondary plant compounds and the effect this has had on the development and diversity of insects.

Biochemical Aspects of Plant Evolution

Southwood (1973), in an extremely perceptive review, pointed out that our knowledge of the changes which have taken place in insect-plant interactions during the course of evolution was expectably incomplete. Thus, while it is reasonably easy to postulate that the recently-evolved lepidoptera (Smart and Hughes 1973) must have co-evolved with the angiosperms (Ehrlich and Raven 1965), it is much more difficult to do the same for other more ancient extant insect and plant phyla. As a contribution to the solution of this problem, I would like to describe the probable overall biochemical changes which have taken place in certain classes of secondary compounds in plants (Table 1) during the course of evolution (Swain 1974, 1976b). It should be noted that, by and large, there has been little change in the compounds or pathways of primary metabolism. All organisms, from bacteria to the most advanced plant or animal, synthesizes the same range of sugars, amino acids, nucleotides, lipids and simple organic acids, using homologous mechanisms and identical biochemical co-factors. The difference between the chemistry of primitive and advanced phyla lies in the diversity of so-called secondary metabolites (Table 1). As has been stressed previously (Swain 1974), most animals synthesize but few such compounds and their evolution is marked by changes in anatomical, morphological and behavioural features. Plants, on the other hand, possess the ability to synthesize a vast range of secondary compounds, the structural diversity of which has increased

Table 1.—Secondary products and their role in plant protection.*

Class	No. of known structures	Example	Afford protection against
Acetylenes	750	Wyerone	Fungi
Alkaloids	4,500	Lupanine	Mammals
Amino Acids	250	Canavanine	Insects
Carotenoids	300	β-Carotene	Photoprotection
Coumarins	150	Scopoletin	Fungi
Cyanogenic glucosides	50	Linamarin	Molluscs
Flavonoids	1,200	Procyanidin tannins	Insects
Glucosinolates	80	Sinigrin	Insects
Lignans	50	Excelsin	Insects
Lipids	100	Waxes	Fungi
Phenolic Acids	100	Vanillic acid	Plants
Polyketides	500	Hircinol	Fungi
Quinones	200	Juglone	Plants
Terpenes**	1,100	Glaucolide-A	Insects
Steroids	600	Ecdysones	Insects
Miscellaneous	500	Tuliposide	Fungi
Proteins	?	Lectins	Insect
Polysaccharides	?	Acylated polysaccharides	Fungi
Other polymers	?	Cutin	Fungi

*Taken from T. Swain, 1976b.
**Excluding carotenoids and steroids.

greatly during the course of evolution (Swain 1974, 1976a). This applies to all classes of secondary compounds from the terpenoids, the non-protein amino acids, the alkaloids and the flavonoids and related compounds to even plant hormones. Before we consider the separate classes of secondary compounds, we should examine the evolution of the Plant Kingdom as a whole (Table 2). Leaving aside the algae and fungi, both of which deserve separate Kingdom rank (Margulis 1976), it can be seen that the green plants, as we know them, arose approximately 400 million years ago with species related to present-day Psilopsida. The ferns and gymnosperms evolved some 25-30 million years later although neither became dominant until the Mesozoic (220 mya). The angiosperms, which are predominant today, only arose in the mid-Cretaceous, some 120 mya and became the major part of the flora by the early Tertiary.

Table 2.—Classification and age of plant kingdom.*

Division** (number of species)	Subdivision	Class	Common name	Age of oldest known fossil (millions of years)
Procyotes				
Schizophyta (1200)		Schizomycetes	Bacteria	3200?
Cyanophyta (1200)		Cyanophyceae	Blue-green algae	2800
Eucaryotes				
Chlorophyta (6500)		Chlorophyceae	Green algae	1000
		Charophyceae	Stoneworts	450
Phaeophyta (1500)		Phaeophyceae	Brown algae	400-600
Rhodophyta (3000)		Bangiophyceae	Red algae	600-900
		Florideophyceae		
Fungi (3200)			Fungi	460
Bryophyta (2300)		Hepaticae (9000)	Liverworts	380
		Anthocerotae (30)	Hornworts	?
		Musci (14000)	Mosses	280
Tracheophyta (297000)	Psilopsida (3)		Psilophytes	400
	Lycopsidea (1300)		Lycopods	380
	Sphenopsida (25)		Horsetails	380
	Pteropsida (295600)	Fillicinae (9300)	Ferms	375
		Gymnospermae (640)	Gymnosperms	350
		Angiospermae (286000)	Angiosperms	120

*Taken from T. Swain 1975.
 **Several algal divisions are omitted.

Evolution of Terpenoids

What corresponding changes have taken place in the evolution of secondary compounds? Let us first consider the terpenoids. This class of natural products, which is by no means confined to plants, consists of a number of different types of compounds which arise from the condensation of two or more C₅ isoprenoids units. They range from C₁₀ compounds, the monoterpenes to polyisoprenoids including the terpenoid quinones and high molecular weight polymers such as rubber. Their route of biosynthesis involves the formation of an active C₅ unit, with subsequent condensations to give the higher C₁₀-C₅₀ oligomers.

Polyisoprenoids, carotenoids (C₄₀₋₅₀) and sterols (C₂₁₋₂₇ from triterpenoid precursors) are ubiquitous in plants and their presence in procaryotes (Table 3) indicates that they arose early in evolutionary time (Swain 1974). However the monoterpenes, so important as alarm and defensive substances in numerous species of insect (Clayton 1970), are more or less absent in lower land plants, the ferns, horsetails, and lycopods which were the predominant forms until the Carboniferous 220 mya. Even the sequi- and di-terpenes show little structural variation until the rise of the angiosperms, in which many have been shown to be feeding-deterrents to a wide variety of insects (Swain 1976b). It appears possible, therefore, assuming insects are dependent on diet for the production of monoterpeneoid pheromones (Hendry et al. 1976, Hendry 1976), that more primitive insects might well have utilized different classes of compounds as pheromones such as the long chain ketones or unsaturated acids and this may be reflected in their progeny today. It is also interesting that the ecdysones, which are found in many ferns occur more commonly in those species which are considered advanced, and which, by and large, also possess a wider range of other potentially deterrent toxic substances (Swain and Cooper-Driver, 1973). Ecdysones have not been found in lower plants. Does this mean that the pre-Carboniferous insect possessed a different hormonal mechanism controlling ecdysis or did the advanced ferns of the Carboniferous and later evolve the means of synthesizing the compounds independently? Certainly the triterpenoid precursors of the ecdysones are widespread in all plants (Table 3).

Table 3.—The distribution of terpenes in plants^b

Division	Terpenoid ^c				Sterols C ₂₁ -C ₂₇	Carotenoids C ₄₀	Quinones (C ₅)
	Mono- C ₁₀	Sesqui- C ₁₅	Di- C ₂₀	Tri- C ₃₀			
Bacteria				(+)	(+)?	+	+
Cyanophyta				(+)	(+)	+	+
Rhodophyta	(+)	(+)			+	+	+
Phaeophyta		(+)			+	+	+
Chlorophyta	(+)				+	+	+
Fungi	(+)	(+)	+	+	+	+	+
Bryophyta		+		+	+	+	+
Tracheophyta	+	+	+	+	+	+	+

^aMany individual species do not contain representatives of each class of terpenoid shown.

^bTaken from T. Swain, 1974

^c(+) means reported in only one or two species.

Evolution of the Tannins

Let us now examine evolutionary trends in the tannins which have been shown to be feeding deterrents to insects and other herbivores in a wide variety of plants (Swain 1976b). The tannins are relatively high molecular weight (1-5 K) phenolic compounds which are ecologically important because they precipitate proteins. This accounts for their astrigent taste which, to us, acts as a cue to

avoid plants which contain too high a concentration of them. If ingested, tannins can inhibit hydrolytic enzymes in the gut and at the same time render proteins present in the diet nutritionally inaccessible, since tannin-protein complexes are not broken down by proteases. They are, therefore, potent inhibitors of animal growth.

The tannins can be divided into two classes chemically, the condensed and hydrolysable tannins. The condensed tannins or proanthocyanidins, are polymers of flavan-3,4-diols, so obviously their evolution depended on the ability of plants to synthesize the related 3-hydroxy flavonoids (Swain 1975). The hydrolysable tannins, are esters of glucose with gallic acid or its congeners, especially the dimer, hexahydroxy diphenic acid, the latter giving rise to the ellagitannins. They are more effective protein precipitants than the condensed tannins but, as their name suggests, are biodegradable. Both types of tannins, it should be noted, arise from the same biosynthetic route *via* shikimate which leads to many other aromatic compounds including lignin.

From the evolutionary point of view, the condensed tannins are first found in the Sphenopsida, the only living genus of which is *Equisetum* (Table 4). This group of plants, together with the lycopods, were the dominant forms in the coal-producing flora, being replaced by ferns and protogymnosperms in the Permian (Swain 1974). It appears likely that the condensed tannins arose as necessary defences against phytopathogenic fungi and bacteria, as plants developed more extensive and complex open vascular systems (Swain 1974, 1975). This is not to say that tannins could not act as deterrents to Paleozoic insects but in fact there appear to be very few herbivores at that time; most of these early insects were either carnivorous or detritus feeders (Smart and Hughes 1973). Perhaps the occurrence of condensed tannins in the Carboniferous flora affected the evolution of herbivorous forms.

Table 4.—Overall distribution of tannins and alkaloids in Cretaceous plants.¹

Taxa	% of Genera examined containing			
	Tannins		Alkaloids	
	Condensed	Hydrolysable	Aromatic ₃	Total
Sphenopsida ¹	28	0	0	0
Ferns	92	0	0	0
Gymnosperms	74	0	0	18
Angiosperms ⁴	54	13	15	29
Dicotyledons	62	18	16	30
Monocotyledons	29	0	4	26

¹ Data from Chesters et al. (1967). Taken from T. Swain 1976a.
² On a species basis.
³ Based on family distribution of alkaloids derived from aromatic amino acids, phenylalanine, tyrosine or tryptophan.
⁴ For comparison the data on post-Cretaceous angiosperms are 31% genera with condensed tannins. 8% with hydrolysable tannins, 11% with aromatic alkaloids and 31% with total alkaloids.

It is interesting that, even today, despite the long association between condensed tannins and the later herbivorous insects, the latter do not seem to have developed any satisfactory detoxification mechanisms against the phenolic polymers. The same is true of course for vertebrates, so even if condensed tannins are ‘old hat’ as chemical defences, they are still remarkably effective. It is probably only the fact that their synthesis and *storage* involves such a high metabolic cost which has made several more recent plant phyla abandon them as defensive agents (Table 4).

The hydrolysable tannins present a different picture. They are found only in the angiosperms, and, indeed, only in dicotyledons. Experiments with reptiles and mammals have shown that they are ca. 5-times more effective, on a weight basis, as feeding deterrents than the condensed tannins (Swain 1976a). Furthermore, analyses of their occurrence have shown that they are present in a larger proportion of genera in more ancient angiosperm families than in more recent taxa. It was suggested, therefore, that the early evolutionary success of the angiosperms in the Cretaceous can be ascribed to their presence, since they acted as more potent feeding-deterrents than the condensed tannins to the ruling reptilian herbivores (Swain 1976a). Again, therefore, it appears that these quite recently evolved compounds were not primarily selected as defences against insects.

Evolution of the Alkaloids

Now let us consider the alkaloids. These comprise of a wide variety of highly toxic nitrogenous bases, which, unlike the terpenoids and tannins, arise from an array of different precursors (Swain 1974). The so-called biosynthetically true alkaloids are formed from six or seven protein amino acids while the psuedo-alkaloids arise by a variety of other routes from polyketides, terpenoids, and so on. These latter compounds are, of course, still perfectly good defensive substances. Almost all alkaloids are, to us, more or less intensely bitter and this enables us, and other mammals, to avoid plants containing them (Swain 1976b).

From the evolutionary point of view it is useful to distinguish between those true alkaloids which arise from the aliphatic amino acids, ornithine and lysine, and those which have as precursors, the aromatic acids, phenylalanine, tyrosine and tryptophan. One can see from Table 4 that the alkaloids like the hydrolysable tannins, are an angiosperm "invention." This is certainly true of the aromatic alkaloids which have not so far been found in any non-flowering plant. This does not mean that lower plants were devoid of nitrogenous defensive compounds. Cyanogenetic glycosides occur in ferns, albeit sporadically, and still provide a hurdle which insect and other herbivores have not been able to fully surmount (Cooper-Driver and Swain, 1976).

It seems probable from their distribution that the alkaloids arose as a defence against mammalian herbivores as these co-evolved along with the angiosperms in the late Cretaceous. This is supported by the fact that the concentration of alkaloids required to deter this class of animals from feeding are 10-30 times less than is required for the reptiles, while many insects and birds appear to be able to tolerate plants containing alkaloids in relatively large amounts (Swain 1976a). The evolution of alkaloidal pathways in the angiosperms, at least, again does not seem to have been called into play by insect pressure even though many of these compounds are today potent insecticides and feeding deterrents (Chapman 1974).

The General Distribution of Secondary Compounds in Plants

Let me now turn briefly to the distribution of defensive chemicals within the plant kingdom. Obviously, not all dicots possess a given class of deterrents. The ellagitannins, for example, are not found in every superorder or even genus (Table 5) and this illustrates the fact that different plants have adopted varying strategies for survival. Even within a single family, various genera may contain

Table 5.—Distribution of tannins and alkaloids in angiosperms.¹

Subclass ²	% Cretaceous ³ Families	% Genera examined containing			
		Tannins		Alkaloids	
		Condensed	Hydrolysable	Aromatic	Total
Dicotyledonae					
Hamamelididae	36	59	26	0	5
Magnolidae	23	56	5	21	27
Rosidae	19	46	28	7	18
Dilleniidae	17	51	18	2	12
Caryophyllidae	13	22	0	8	16
Asteridae	11	13	1	8	27
Ranunculidae	9	17	3	69	69
Monocotyledonae					
Arecidae	29	52	0	0	25
Liliidae	15	18	0	6	30
Commelinidae	14	11	0	0	9
Alismidae	9	33	0	0	0

¹ Taken from T. Swain 1976a.

² According to Takhtajan (1969).

³ Families with a fossil record prior to 65 million years ago; data from Chesters et al. (1967).

different types of toxic compounds as defensive substances as is shown by the distribution of alkaloids in the Apocynaceae. Here, the 84 genera in the sub-family Plumerioideae almost all contain only complex indole alkaloids whereas the 56 genera in the Echitoideae have steroidal alkaloids: the 3 genera in the third sub-family, Cerberoideae contain neither of these classes but have simple pyridine derivatives. One cannot, therefore, assume there is likely to be some general homology in the range of insects and their detoxification mechanisms for every member of a given family of plants as is implied by studies on the Cruciferae (Schoonhoven 1973). The dangers of generalizations about the relationship between insect and plant species is perhaps more readily seen when one examines the well known factor of biochemical genetic polymorphism. Many cyanogenetic species exhibit this feature (Jones 1972) in which a fraction (0-100%) of the individual plants in a given population produce the toxic gas HCN on crushing, the rest being acyanogenic. This situation reminds one of insect mimicry (Rothschild 1973).

Even within a single plant there can be wide variation in concentration of a single toxin both in space and time. For example, cyanogenesis in bracken is high in young fronds and almost non-existent in older leaves and there are marked variations in the production of HCN even along a single frond of the mature plant (Cooper-Driver and Swain 1976). Similarly, in cassava, young leaves produce more HCN than older leaves and the production is dependent on the turgidity of the leaf. On wilting, less HCN is produced and this correlates with the acceptability of the leaf to locusts (Bernays and Swain 1976).

It should also be noted that climatic and edaphic conditions also affect the production of secondary compounds; shade plants usually produce much lower amounts of secondary compounds than those growing in the sun (Swain 1976a). There are also often wide diurnal or even hourly variations in the concentrations of certain secondary compounds in different plant organs. This demonstrates that such compounds are continually being turned over and cannot be regarded as waste products (Swain 1976c). It seems possible that the plant might benefit by exhibiting a rapid variation in toxins, since by giving out different signals at different times it might avoid herbivore fixation. Another factor which needs to be taken into account when considering the concentration and distribution of secondary compounds is their induction by phytopathogens and even by insect damage (Swain 1976b). The intensity of these reactions and their effect on both insect and plant have not been fully explored, but what is known indicates their importance (Osborne 1973).

General Conclusions on the Biochemical Aspects of Plant-Insect Co-evolution

It can be seen from the earlier sections of this review that many organisms have had a profound effect on the chemical defences of plants during the course of evolution, but that it appears insects probably had little say in the matter until the Cretaceous. Indeed it seems more likely that plants have had a much greater effect on insect evolutionary strategies in a chemical sense than vice-versa, and this is to be expected since it is the plants which provide the chemical arsenals, hormones, pheromones and so on, which determine the success of the insect. This is not to say that there has not been a rather rapid biochemical co-evolution taking place during the last 70-80 million years between insects and angiosperms which has been extremely important in determining the diversity of present-day ecosystems. But it should be noted that the effects of this co-evolution appear to have been mainly on increasing the heterogeneity and number of secondary compounds within a given class rather than determining the evolution of the biosynthetic pathways leading to that class. In some cases, even the heterogeneity of secondary compounds does not seem to have been called into play by insects, as witness the large number of glucosinolates which can act as attractants for *Pieris brassicae* and other species (Schoonhoven 1972). Nevertheless, it appears obvious that the challenge which insects have afforded plants has led to a much wider range of intertwined biochemical reactions than would have been the case if the only herbivores were vertebrates and molluscs.

The short exposition regarding the variation in secondary products in plants, both between and within species, hopefully will draw attention to the complexities of the situation which does not always seem to have been appreciated. These aspects of plant science received scant attention until about 15 years ago and, even today, there are few reference works (e.g., Hegnauer 1961-76, Miller 1973) which cover the field adequately. Insect physiologists and behaviourists need to be on guard also regarding the variations of plant chemicals on space and time, so that the overall biochemical complexity of insect-plant interactions can be properly unravelled. I hope that this short review will reinforce the excellent start (e.g., Chapman 1974, Clayton 1970, Ehrlich and Raven 1965, Feeny

1975, Gilbert and Raven 1975, Hendry 1976, Janzen 1975, Kogan 1976, Osborne 1973, Rothschild 1973, Schoonhoven 1973, Southwood 1973, Städler 1976, Van Emden 1973) which has been made on seeking solutions to these problems.

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The Physiology of Hematophagous Insect/Animal Host Relationships

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ABSTRACT

Location of the host involves orientation based on vision, heat, CO₂, water vapor and olfaction stimuli. Polyphagous parasites are attracted mainly by CO₂ and several sweat components, especially lactic acid. Mono- and oligophagous parasites are attracted by specific, so far unidentified host kairomones, usually enhanced by CO₂. Attachment to host and probing are affected by physical and chemical attractants and deterrents of host skin. All hematophagous arthropods studied were found to be stimulated to gorge by adenine nucleotides or reduced glutathione. Insects identify blood by the adenine nucleotides released from blood platelets which aggregate in the region penetrated by the parasite.

The level of some B vitamins is very low in blood of many vertebrates. A wide variety of blood sucking arthropods possess symbiotic microorganisms which supply the deficient vitamins. Species which do not possess symbionts exhibit normal development only on a limited host range.

Host specific ectoparasites often encounter difficulties in digesting 'foreign' blood.

Exposure of host to parasite often triggers an immune response, resulting in rejection of the parasites on subsequent exposures.

The following abbreviations are used in this paper:

ADP	adenosine diphosphate
AMP	adenosine 5-monophosphate
cAMP	3',5'-cyclic adenosine monophosphate
ATP	adenosine triphosphate
CDP	cytidine diphosphate
CTP	cytidine triphosphate
DPN	diphosphopyridine nucleotide
DPNH	reduced diphosphopyridine nucleotide
FAD	flavin adenine nucleotide
GDP	guanosine diphosphate
GMP	guanosine monophosphate
cGMP	3,5-cyclic guanosine monophosphate
GTP	guanosine triphosphate
IDP	inosine diphosphate
IMP	inosine monophosphate
ITP	inosine triphosphate
GSH	reduced glutathione
UDP	uridine diphosphate
UTP	uridine triphosphate

Hematophagous arthropods display host specializations equaling those of phytophagous insects. Under natural conditions the parasite may encounter only a very limited range of its possible hosts, and specificity appears narrower than it really is. To that extent the ecology and ethology factors

which determine the possibility of contact between the parasite and the host may be considered to influence specificity. We therefore differentiate between normal and potential host spectra. The latter term refers to the absolute suitability of potential hosts and not to the natural situation. The natural host spectrum is an expression of the actual situation at a particular time and place. The complete host spectrum has not been worked out for any parasite (Levine 1973).

My presentation will concentrate on the physiological basis of host ectoparasite relationships and will not deal with the host ecology or ethology.

The physiological factors can be divided into three major categories:

- (a) The role of kairomones and allomones in host selection,
- (b) the role of nutrients in host-insect interactions, and
- (c) food utilization as a factor in host specificity.

1. Host kairomones and allomones

As in phytophagous insects, host selection by hematophagous insects depends on characteristic pattern of stimuli.

Finding the Host from a Distance. — Usually involves orientation based on vision, heat, CO₂, water vapor and olfactory stimuli, emanating from the prey. Odor seems to override other cues in the hierarchy of attractive stimuli (Khan et al. 1966). In flying insects, location from a distance is important in host selection. While polyphagous parasites are attracted to odors which are important components of sweat of all warm-blooded animals, the monophagous insects react to specific host odors. CO₂ activates or attracts almost all blood feeders that were tested. This includes mosquitoes, black flies, midges, tabanids, fleas, ticks and mites (for review see Galun 1976).

Lactic acid, the major sweat component, is another important host kairomone. It attracts mosquitoes very strongly (Acree et al. 1968), but probably is an attractant to other blood feeders as well. Bernard (1974) identified a receptor on the antenna of *Triatoma* which responds very distinctly to physiological concentrations of L-lactic acid.

Neither visual stimuli, nor thermal ones, nor CO₂ could account for any host specificity. Oligophagy or monophagy exhibited by many arthropods could probably be mediated through *kairomones* emitted by the host. In arthropods, only the olfactory sense has the versatility to account for specificity. Though much effort has been devoted to find specific attractants, the chemical identity of any of the host kairomones responsible for attracting host specific parasites from a distance, is not yet known. However it has been often shown that hosts extract could attract specific ectoparasites from considerable distance. Such a phenomenon was very elegantly demonstrated by Fallis and Smith (1964) with ornithophilic simuliids.

Simulium euraydimiculum is monophagous — feeds exclusively on the common loon (*Gavia immer*). This fly shows a very strong attraction to ether extract of the uropygial gland and tail of the loon. Extracts of other birds have no effect.

Simulium rugglesi feeds readily on ducks and to a limited extent on birds that frequent the forest canopy and thicket. They are attracted to extracts from duck gland plus CO₂, to a lesser extent to CO₂ alone, but not in the extract alone. *S. aureum*, *S. latipes*, *S. quebeceuse* and *S. croxtoni*, with less specific host preference are attracted in considerable numbers to CO₂ alone.

Host Probing and Sampling of Diet. — Once an insect is in actual contact with a possible source of food, it is in a position to test it with its mechanoreceptors and contact chemoreceptors on the tarsi and mouthparts.

The physical factors of the host skin, as well as temperature and humidity are the major factors which induce or depress probing (Gatehouse 1970, Margalit et al. 1972). Host selection at this level is probably associated with the presence of deterrents in the skin of various hosts. Thus, while polyphagous ticks will feed on various mammals and hosts, ornithophilic ones are very reluctant to feed on non-avian hosts. When the fowl tick or the poultry red mite are offered non avian blood they engorge in vitro only through bird skins regardless of the source of the blood. A certain amount of feeding is observed also on inert membranes but not on non host skins indicating that the deterrent factors of "foreign hosts" are apparently more important than attractants of the favored hosts (Galun 1976, Kirkwood 1971). This is further supported by the fact that the red poultry mite will feed on bird skin which has been preserved in alcohol for several months.

After probing, two distinct phases can be observed in the feeding process of many blood sucking insects. The first is the questing, sampling or tasting phase. During this phase, a little blood is

sucked into the cibarium. When the presence of the blood (or rather the specific phagostimulants in it) is recognized by cibarial receptors, continuous pumping is initiated and the second phase, the continuous feeding or gorging, commences. The first phase was described for *Rhodnius*, mosquitoes and tsetse flies (Friend and Smith 1971, Owen 1963, Margalit et al. 1972). In *Rhodnius* at irregular intervals during maxillary probing the diet is sampled by several 1-6 pulsative movements, which represent 'trial activity' of the pharyngeal pump. One to three sampling periods during 10-20 sec occur when the insect is exposed to an acceptable diet. On a saline diet containing no gorging factor, the insect continues to sample the diet for a longer time, sometimes withdraws the stylets completely and then reinserts it and commences probing and sampling. In tsetse flies non-stimulatory diet such as water or saline is not sampled after probing. Proboscis is withdrawn and reinserted into non stimulatory solutions at very high frequency. The presence of ATP in diet was shown to be needed to initiate intermittent cibarial pumping, which sucks the diet up to the cibarium.

Mosquitoes and *Rhodnius* do not possess any chemoreceptors on those parts of the proboscis which come into contact with the host or the diet during the initial probing-tasting phase. Sampling is probably induced by the same factors which induce probing, and sampling would enable the diet to come in contact with the receptor cells which are internal to the food canal.

In tsetse flies the two phases of feeding could be associated with the two distinct groups of sensory receptors found on the mouth parts of the fly. The external labial receptors govern the probing and tasting while the internal labrocibarial receptors govern the regular pumping and gorging. The four long thick seta arising from sockets situated between the prestomal teeth of each labellum containing 2 chemoreceptor cells each, were proposed by Rice et al. (1973) as monitoring the tissue and blood ATP — the tasting stimulus of the fly. These sensilla are situated such that with each new eversion of the labella they will make contact with the tissue ahead. Recently electrophysiological recordings have been made from these cells, indicating a response specific to ATP over a concentration range of 10^{-6} - 10^{-3} M (Mitchell 1976).

Maintained Feeding or Gorging. — Once the presence of the blood is recognized by the epipharyngeal or labrocibarial receptors, continuous regular pumping is initiated and feeding is maintained until abdominal stretch receptors provide a negative feedback to the imbibition of blood. By means of artificial feeding of various blood fractions and blood components, the blood factors which initiate gorging have been identified for many parasites. Some data are presented in Table 1.

As seen from the table all the blood sucking insects use adenine nucleotides as gorging stimulants. The specificity of the phagostimulatory compounds tends to narrow with evolution. While the primitive acarines are stimulated most effectively by reduced glutathione (GSH), a variety of purine nucleotides and several amino acids, the blood sucking insects limit their response mainly to adenine nucleotides, with ATP and ADP being most effective for all.

ATP and glutathione are found in cells of all living organisms and in spite of the considerable variations between animals in their concentrations (Table 2), their level is always many fold higher than the stimulatory threshold. The ATP concentration required to induce 50% of *Rhodnius* or *Glossina* to feed is between 10^{-5} - 10^{-6} M. Once they start feeding they consume a full meal regardless of the concentration of the stimulant (Table 3).

Thus, variations in concentrations of the phagostimulants could not account for variations in feeding response on the various hosts. Yet, the high concentration of ATP in blood is very misleading as it is all confined to the cellular fraction of the blood, where it is firmly bound, and thus it does not gain egress to the blood detecting chemoreceptors. Galun and Rice (1971) found that the intact red blood cells indeed do not stimulate gorging, and blood is detected by the adenine nucleotides released from blood platelets, which aggregate in the bitten region due to the damage done to blood capillaries by the probing proboscis. Platelet aggregation is a response to ADP (Gaarder et al. 1961). The ADP comes initially from injured vessel walls and then from the platelets themselves, through a release reaction initiated by the ADP (Käser and Glanzman 1962).

Host preference through differences in host platelets is a possibility that merits investigation. Clearly, it is not a matter of adenine nucleotides content, but of many other properties of platelets, such as platelets adhesion and spreading on foreign surfaces, release reaction and aggregation etc. There exists evidence for quantitative and qualitative differences in these features, in platelets of various species.

Hematophagy, which is common in many groups of arthropods, has evolved independently in the various groups probably from plant feeders' ancestors. It is therefore quite surprising that all of them have developed along the same line in their gustatory specificity, i.e., being stimulated to feed

Table 1.—Chemical nature of phagostimulants in hematophagous arthropods.

Soft ticks (<i>Ornithodoros, tholozani, O. moubata, Argas persicus</i>)	GSH > ATP = DPNH > ADP > ITP = GTP > AMP, leucine, isoleucine, alanine, phenylalanine, proline, (each in the presence of glucose).	(Galun and Kindler 1965, 1968)
<i>Rhodnius</i>	ATP > ADP = CTP = GTP = CDP = ITP > cAMP > IDP = GDP > AMP UTP, UDP, Riboflavin 5 — phosphate Creatine phosphate, tetrasodium pyrophosphate	(Friend and Smith 1971) (Friend 1965)
Mosquitoes <i>Culex pipiens</i>	ADP > AMP > ATP	(Hosoi 1959)
<i>Aedes aegypti</i>	ATP > ADP = DPN = FAD > AMP	(Galun 1967)
Tsetse fly <i>Glossina austeni</i>	ATP > ADP > AMP = cAMP	(Galun and Margalit 1969)
Black flies <i>Simulium venustum</i>	ADP > ATP*	(Sutcliffe and McIver 1975)
Rat flea <i>Xenopsylla cheopis</i>	ATP	(Galun 1966)

*Other compounds not tested.

Table 2.—Content of some phagostimulants of blood of various animals (mg/100 ml).*

	Man		Cattle		Rabbit		Pigeon	
	Cell	Plasma	Cell	Plasma	Cell	Plasma	Cell	Plasma
ATP	72	0	27	0	112	0	182	0
GSH	77	0	157	0				
Glucose	74	97	15	85	41	145	150	
Isoleucine	0.9	1.6						
Leucine	1.5	1.9						

*From Albritton 1952.

Table 3.—Regulation of feeding of *Glossina Austeni* as a function of the concentration of ATP.

Concentration of ATP	No. of flies	Meal size (mg)	Avg. feeding time (seconds)	Rate of feeding mg/sec
10 ⁻⁵ M	24	15.0	34.3	0.44
10 ⁻⁴ M	19	16.7	43.0	0.39
10 ⁻³ M	20	18.0	36.0	0.50
10 ⁻² M	21	18.4	50.0	0.37

by either GSH or adenine nucleotides. If chemical activation of the feeding response is an adaptive characteristic, the adaptation to these compounds would seem logical because they are abundant in blood of all animals. Yet, the fact that they are confined to blood cells and therefore are not freely available to the chemoreceptors of the parasite means that additional evolutionary adaptations were required in order to develop an effective detection mechanism. It is probably logical to assume that the adaptive value of these compounds stems from the fact that they are extremely effective at the molecular level of interaction with the chemoreceptor membrane. If this assumption is valid, and since GSH and adenine nucleotides are very abundant in plant tissues, we would expect the feeding of phytophagous insects also to be stimulated by these compounds.

While the phagostimulatory effects of basic nutrients such as sugars and amino acids were studied in many phytophagous insects, the observations on the stimulatory effect of purines, pyrimidines and their nucleotides are very limited, probably due to the fact that they are common to all plants and would not explain monophagy or oligophagy.

Hsiao (1969) provided the first recognized case of a phytophagous insect that responds to free purine- or pyrimidine related compounds. He identified adenine and adenosine as the feeding stimulants inducing the alfalfa weevil to eat alfalfa leaves. ATP, ADP and AMP also elicit feeding response in the weevil, though to a lesser extent. A few years later, adenosine was identified as the feeding stimulants of the sweet-clover weevil. Adenine, which was most effective for the alfalfa weevil, was not stimulatory to the sweetclover weevil. A slight stimulation was shown also by ATP but not by any other purine or pyrimidine bases or nucleotides (Beland et al. 1973).

Recently Ma (personal communication) identified adenosine isolated from maize as a most effective feeding stimulus for the African army worm (*Spodoptera exempta*). In electrophysiological studies he identified a receptor in the lateral maxillary peg which was highly specific to adenosine. In comparative studies with *Spodoptera littoralis* and *S. furgipetra* an identical adenosine receptor was found.

The omnivorous housefly is stimulated to feed by guanine nucleotides, but not by nucleotides of other bases (Robbins et al. 1965). I tend to believe that a methodical study on the role of purines and purine nucleotides in the feeding of various insects will increase this list many fold.

The suggestion that GSH and purine nucleotides are extremely effective chemotactic agents finds further support from the behavioral responses of organisms at all evolutionary levels to these compounds.

GSH is a specific feeding incitant in several hydrozoans including fresh water hydra, marine hydroids and siphonophores, and in anthozoans such as corals, anemones and zoanthids (for review see Lindstedt 1971, Reimer 1973).

cAMP released from bacteria into the medium attracts slime molds to them; thus even this primitive organism is using this chemical clue as a part of its feeding behavior (Konijn et al. 1969). At a different phase of their life the cells of the slime mold start secreting cAMP which causes their aggregation (Konijn et al. 1967). The nematode *Caenorhabditis elegans* which feeds on bacteria is also attracted to their food by cAMP and cGMP released by these bacteria.

The histophage ciliate *Orphyoglena* is attracted to its prey by RNA, DNA, ATP released from broken prey animals.

Chemostimulation by purine nucleotides was described also in human beings. 5-GMP and 5-IMP have very agreeable taste and are used as flavor enhancers for proteinaceous food for man. The flavor enhancing ability is very specific. Free purine and pyrimidine bases, nucleosides and polynucleosides have little recognizable taste (Kuninaka 1960). Purine nucleotides are used as chemotactic agents also in suborganismic levels. As previously mentioned, blood platelets aggregate to form a thrombus as a response to exogenous ADP. cAMP is chemotactic to rabbit peritoneal neutrophils (Rivkin and Beeker 1976).

Studying the interaction of the stimulant with the specific chemoreceptors which initiate gorging in blood sucking insects is very difficult. Electrophysiological studies are complicated because these suspected receptors are internal to the food canal and extremely small.

The epipharyngeal sensilla in the roof of the food canal anterior to the pharyngeal pump in *Rhodnius* and *Triatoma* are the most likely ones to respond to the blood ATP (Friend and Smith 1971b). These sensilla were described by Bernard (1974) as 11 tiny domes, about 1 μ in diameter, each having a slit in the center, through which microelectrodes for recording should be inserted. Bernard failed to do electrophysiological recordings from these sensilla because the area is densely innervated by the nerves coming to the pharyngeal pump muscles.

In the tsetse fly the only chemoreceptors within the food canal which could taste the food before it enters the alimentary tract are 4 basiconic pegs set into the dorsal edge of the posterior cibarial wall. Each of these sensilla possesses a single neuron (Rice et al. 1973b). Thus there are only 4 cells which monitor the presence of ATP in the fly diet, and fire impulses to the tritocerebrum, from which the motor impulses pass out to instigate continuous cibarial pumping. Owing to the very small size of these labrocibarial receptors, and to their location, Rice et al. (1973b) could not record directly from this receptor in order to produce electrophysiological evidence for their specificity.

Due to the small number of these receptors, it is also very doubtful if any biochemical work of the specific receptor membrane proteins could ever be carried out in arthropods.

2. Role of Nutrition in Host Specificity

Fraenkel (1969) in an earlier symposium on the same subject argued against the role of nutrients in host selection by phytophagous insects. As he stated it, the qualitative nutritional requirements of all insects are by and large the same, and differ only little from those of higher animals. The 30-40 substances which are involved in insect nutrition are constituents of all living cells, and therefore we may assume that they are all found in blood cells of all animals.

Blood is rich in proteins, but the amino acid composition is quite different from plant proteins (Table 4). While blood proteins are very rich in leucine, lysine and histidine, they contain little isoleucine.

Table 4.—Approximate amino acid composition (%).*

Amino acid	Whole blood	Globins and Hemoglobins	Alfalfa meal	Whole wheat
Arginine	4.5	3.3	4.9	4.3
Histidine	6.4	7.6	1.8	1.8
Lysine	9.2	9.3	5.0	2.5
Tyrosine	2.5	2.9	2.9	3.6
Tryptophane	1.4	1.5	1.3	1.2
Phenylalanine	7.7	7.6	4.2	4.4
Cysteine	1.4	1.0	1.6	3.3
Methionine	1.2	1.5	1.0	1.2
Threonine	4.4	5.9	5.1	3.9
Serine	8.4	5.3	4.3	3.8
Leucine	11.6	14.5	7.2	6.9
Isoleucine	2.3	0.8	4.6	4.4
Valine	8.3	9.4	4.7	4.5
Glutamic acid	9.8	8.0	8.0	31.4
Aspartic acid	12.4	10.0	14.9	3.8
Glycine	4.7	5.4	4.8	3.4
Alanine	1.0	9.0	5.5	3.0
Proline	4.9	4.8	4.0	10.3

*Data from Block & Weiss 1956.

Unfortunately so far not a single strictly blood feeder has been reared successfully on a chemically defined diet. So we cannot tell whether hematophagous insects have developed through evolution different requirements for amino acids balance, and whether this balance is in accord with the composition of the host blood.

Blood is deficient in certain B vitamins which are essential for insect development. Many blood sucking arthropods established symbiotic relationships with various microorganisms. However, the common notion that all exclusive blood feeders are equipped with symbionts is probably an overgeneralization.

The situation of a consistent bacterial association reported by various investigators for *Rhodnius prolixus* does not appear to hold true for other triatomine species (Nyirady 1973). Yet both *Rhodnius* and *Triatoma* require the presence of intestinal bacteria for their normal development when reared on certain laboratory animals (such as rabbits) while both could develop in a normal manner in the absence of bacteria when nourished on a suitable host (such as mouse). Some differences between composition of mouse and rabbit blood are shown in Table 5. These data do not necessarily reflect the essential missing requirements, but indicate the wide range of concentrations that could be found in blood components between various animals.

Table 5.—Content of various nutrients in blood of several animals.*

	Free Choline mg/100 ml plasma	Panhotenic acid mg/100 ml blood	Total Cholesterol 100 mg/100 cc plasma
Man	6	31	140-260
Cattle	4	200	50-230
Rabbit	0.5	70	35-53
Mouse	5	385	
Chicken		45	125-200

*Data compiled from Albritton 1952, Long 1961, Altman and Dittmar 1974.

It appears that the usual association of *Rhodnius* with its symbionts is related to the low degree of host specificity in that bug and the ability of the microorganism to supply necessary factors when the bug is feeding on an inadequate hose (Auden 1974). On the other hand, *Triatoma protractor* and *T. rubida* which do not have consistent bacterial flora have a limited host range in nature, feeding usually on wood rats. It may perhaps be assumed that wood rats (*Neotoma* sp.), like the mouse, could support normal development of aposymbiotic *Triatoma* (Nyirady 1973). The bugs will indeed feed on other animals when exposed to them, but many hosts like the rabbit will presumably not support their normal development and reproduction.

3. Blood Utilization

To what extent the source of blood is instrumental in limiting the host range has never been thoroughly investigated. Among host specific ticks, blood imbibed from non host animals does not always appear to be agreeable to ticks. Thus the few fowl ticks, *Argus persicus*, which were induced to imbibe on rabbit or on guinea pig, or *A. arboreus* on guinea pig, often turned purple and died (Galun 1976, Tawfic and Guirgis 1969). It would be unreasonable to assume that rabbit blood contains toxic factors for *Argas*, while it is quite suitable for closely related species of ticks. The biophysical and enzymatic characteristics of parasites as apply to “foreign” blood are unknown. We have observed for example that even a slight hemolysis of the blood prior to feeding it to soft ticks, causes 100% mortality of the ticks, indicating that rate hemolysis of the ingested blood could be a crucial factor for survival. Thus fragility of blood cells may play a role in host specificity.

Similar lethal effects of “foreign” blood were described in some monophagous lice. *Pediculus atelophilus* from spider monkey died without digesting the blood after feeding on man (Ewing 1933). *Pediculus humanus* died after feeding on guinea pig — presumably due to build up of large pyramidal crystals within the midgut causing rupture of this organ (Krynski 1952). Nelson et al. (1975) found similar crystals in many anopluran feeding on guinea pig, while feeding on rabbit produced lumpy agglutinations.

During their feeding on the host the parasites inject antigens which provoke or stimulate immunological resistance mechanism in the host. This aspect is of special importance in parasites which are in contact with the host for many days or months, such as ixodid ticks or louse flies (*Hippoboscidae*).

The best studied case is the resistance of the Zebu cattle (*Bos indicus*) to the cattle tick *Boophilus microplus*. Roberts (1968) has shown that Zebu cattle infested for the first time with

Boophilus are initially highly susceptible. After a few days of exposure to ticks a degree of resistance is acquired. On resistant cattle only a few ticks reach maturity, and most of the larvae are rejected within 24 hrs after attachment due to the immune response of the host. Such rejection might result from damage to the larvae by host factors imbibed, neutralization of digestive enzymes, or alternation in attachment site so that it becomes unsuitable for feeding.

The potential of the animal to develop resistance to ticks is inheritable — and differs between breeds of cattle — being very high in *Bos indicus*. Thus while large numbers of *Boophilus* ticks are found on European stocks (*Bos taurus*), hardly any ticks are found on the Zebu cattle even in heavily infested areas.

In conclusion it may be said that the physiological mechanisms responsible for host selection are similar in phytophagous and hematophagous insects. The differences lie in the ability of the host to develop protective measures. Unlike plants, animal hosts have a potential to develop antibodies which affect the development and reproduction of the parasite. Furthermore, animals are more diversified in their behavior than sessile plants and many vertebrates have developed evasive behavior patterns which are reflected in the natural host range.

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Chemical Exchanges Between the Mouth Parts of Ticks and Their Hosts

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ABSTRACT

The interconnections between insect/plant and tick/animal host relationships are discussed. The tick's feeding process and the host's nutrient contribution are considered. The morphology of the tick's salivary glands and their function in the secretion of cement, in developing the feeding lesion in the host, in elimination of water, salts and waste products, in secretion of pharmacologically-active, toxic and antigenic substances are described, together with the host's reaction to this intrusion. Special mention is made of the antigens in the saliva of the cattle tick *Boophilus microplus* which can be fractionated to give a number of components with cutaneous anaphylactic activity, and the isolation of a prostaglandin from this saliva.

The evolution of the intimate relationships between ticks and their natural hosts may have been a long one. Just how long is difficult to judge since no fossil records of these soft-bodied animals appear to have been discovered. Hoogstraal (1965) has suggested that ticks developed as parasites of reptiles in the late Paleozoic or early Mesozoic Era based on his observation that seven of the eight structurally primitive haemaphysalid species known today feed on lizards. The oldest specimen of an ectoparasite we have, is that of a louse, *Neohaematopinus relictus* Dubinin, estimated to be ten to twenty thousand years old, discovered on a ground squirrel in the permanent ice at Indigirskiy in eastern Siberia (Dubinin 1948). The earliest historical record of what appear to be ticks is on a 3500 year old fragment from tomb no. 155, Dra Aba-el-Nago, Western Thebes, Egypt, depicting a part of the head of a "hyena-like" animal with three excrescences in the pinna. That these were ticks was inferred by Arthur (1965) who considered the illustration not incompatible with current observations. If this assumption is correct it is the first representation of the interaction which is the theme of this symposium, but the earliest undoubted depiction of a tick is a pottery model from the Nok culture (c500BC-cAD200) from Nigeria (Hoeppli, 1969).

How does my contribution, which will be dealing mainly with the cattle tick *Boophilus microplus* (Canestrini) and its host, fit into the general theme of this meeting, where some speakers are dealing with insect/animal and others insect/plant relationships? Ticks and sucking insects may have evolved in much the same way with respect to their mouthparts. As Sprent (1963) pointed out "Thus the monogenetic trematodes, the leeches, the ectoparasitic crustacea, the ticks, and the ectoparasitic insects, such as fleas, sucking lice and blood sucking flies, all have become specialised for the act of sucking the host's blood or tissues. They have thus become quite distinct from their freelifing relatives and resemble each other in the special development of sucking mouth-parts. It should be noted that some of the blood sucking insects, e.g., bugs, tabanid flies, and mosquitoes, may have derived their blood sucking habits from feeding on plant juices; thus male mosquitoes are exclusively plant feeders, while female mosquitoes are often blood suckers." Thus we, in the symposium, have our interlinked and complementary interests, and experience in one field may have relevance in another.

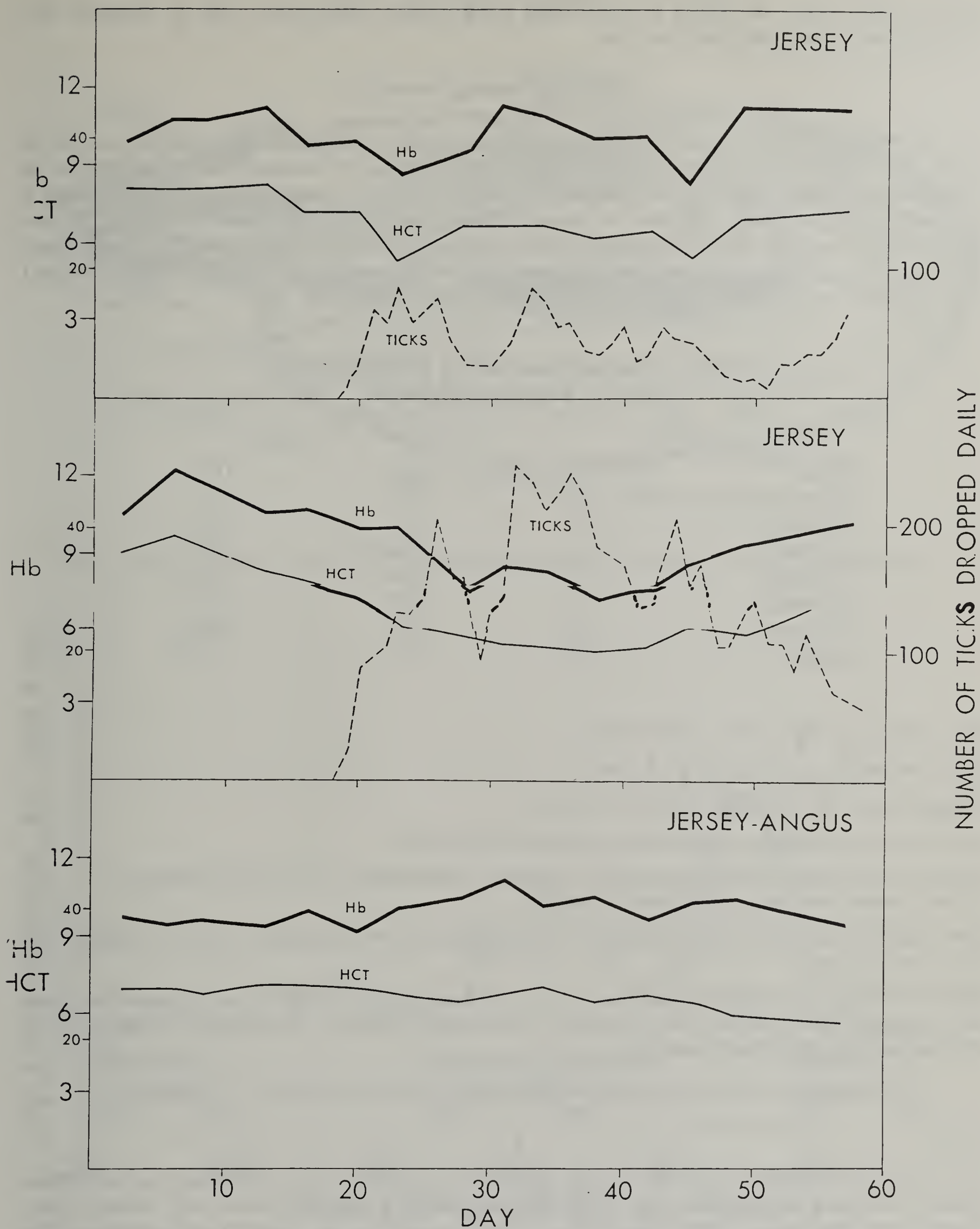


Fig. 1. —The effect of infestation with 1000 larvae per day on the haemoglobin and haematocrit values of two Jersey calves compared with non-infested Jersey-Angus control.

Tick-Host Relationships

No attempt will be made in this short review to be comprehensive and to discuss all ticks and their interactions with all hosts. A number of excellent review articles have appeared to which the reader is referred, notably Nelson, et al. (1975), Hocking (1971), Arthur (1962, 1965). Rather, recent

work, mainly from our group at the CSIRO Long Pocket Laboratories, will be discussed and correlated with work published elsewhere.

The Tick Feeding Process

B. microplus, the tick we have studied most in Australia, is a one-host tick, spending the part of its life cycle from initial attachment as a larva to engorged female or deceased male on the host. As an ixodid tick it represents those species which feed slowly, unlike the argasids whose feeding behavior is relatively rapid and more like that of insects. Those chemical factors which stimulate its host attraction and perhaps determine host specificity have not been determined. Such factors, for blood sucking arthropods in general, has been discussed by Dr. Galun (1976) in this symposium. Rather, I will deal with those substances known to pass between parasite and host.

Table 1. Chemical Composition of Bovine Blood
(approx. percentage by weight)

Water	81	Na ⁺	0.15
Haemoglobin	11	Cl ⁻	0.1
Albumin	3	CO ₃ ⁻⁻	0.1
γ globulin	2	Glucose	0.05
α globulin	1	Urea	0.015
β globulin	1	Ca ⁺⁺	0.01
Fibrinogen	0.5	PO ₄ ⁻⁻⁻	0.006
Lipids	0.3	K ⁺	0.005

Other metals, e.g. Mg⁺⁺, Cu⁺⁺, Fe⁺⁺⁺, Co⁺⁺

Other non metals, e.g. SiO₃⁼, SO₄⁼, I⁻, Br⁻, F⁻

Vitamins, e.g. A, B₁, B₂, folic acid, B₁₂, C, D₂, E

Hormones, e.g. oestrogens, progesterone, androgens, thyroxine.

Enzymes, e.g. amylase, alkaline phosphatase, arginase, transaminases, isocitric dehydrogenase, catalase, choline esterase, prothrombin → thrombin.

Other organics, e.g. nucleotides, bilirubin, serotonin, histamine, prostaglandins, adenosine triphosphate, diphosphoglycerate.

Cell components, e.g. erythrocyte stroma, thrombocytes, neutrophils, lymphocytes, monocytes, eosinophils, basophils; giving nucleic acids, histamine, slow-reacting substance of anaphylaxis, sulphatases and a large number of other chemicals.

Based on Altman and Dittmer (1961), Coles (1974), O’Kelly et al. (1971).

The three parasitic instars of the tick apparently derive their main sustenance via the feeding lesions established in the host’s skin below the tick’s mouthparts (Moorhouse and Tatchell 1966, Tatchell and Moorhouse 1968). Some idea of this transfer can be gained from considering the composition of bovine blood. At the early stage of attachment they would be obtaining tissue juices mainly, but as the lesions develop leucocytes and erythrocytes as well as serum constituents — proteins, carbohydrates, lipids and a wide range of small molecules would pass from the host to the tick Seifert et al. (1968).

This loss of nutrient by the host may be quite severe as indicated by the marked drop in haemoglobin values of the animals as shown in Fig. 3. The results obtained in these individual cases reflect those observed on 21 steers by O’Kelly et al. (1971), examined with full statistical treatment. The digestion of haemoglobin by the adult female tick is a slow process taking about 13 days (Kitaoka 1961, O’Hagan 1974).

CATTLE TICK ORGAN SYSTEM

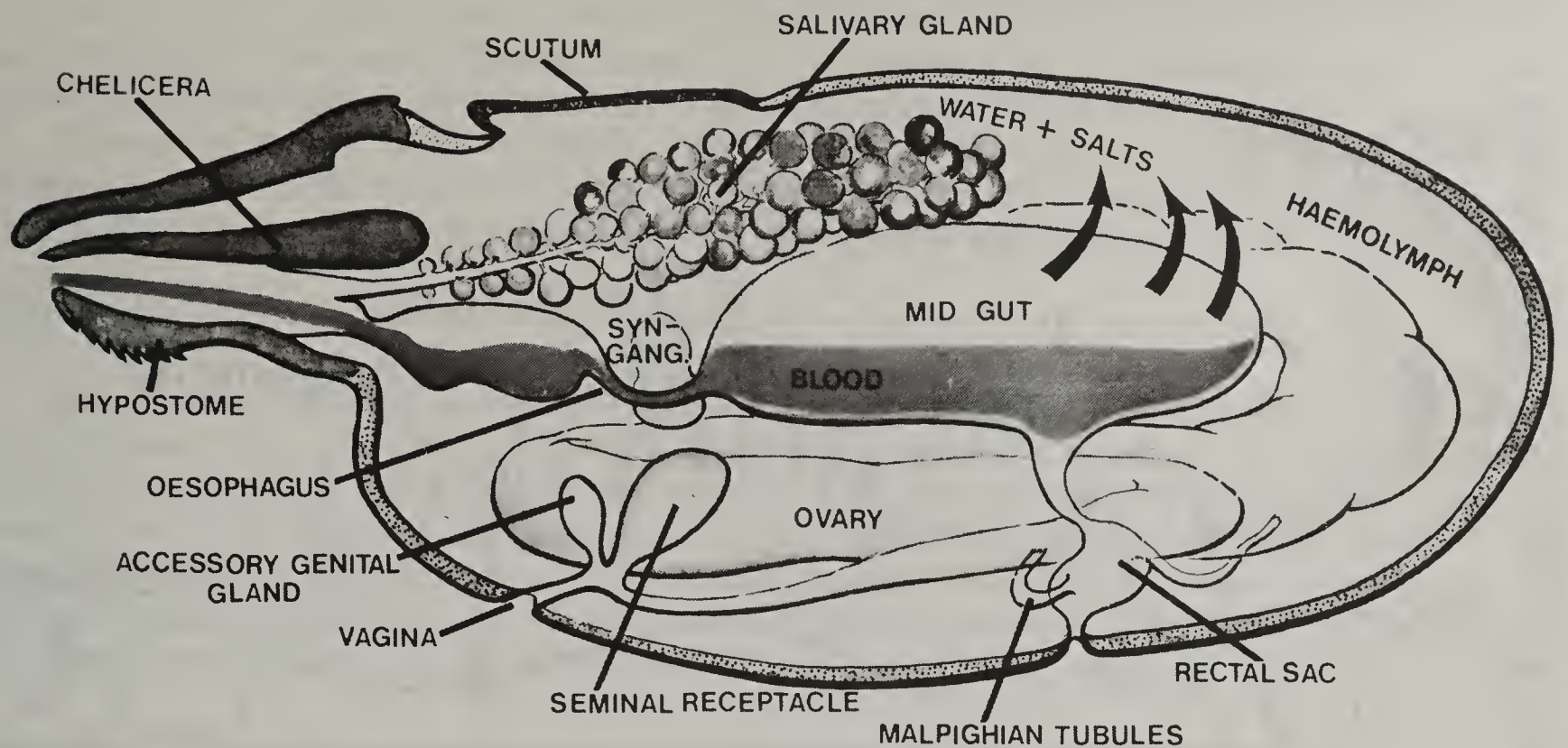


Fig. 2. –Anatomy of the cattle tick showing the position of the salivary gland (Binnington, unpublished).

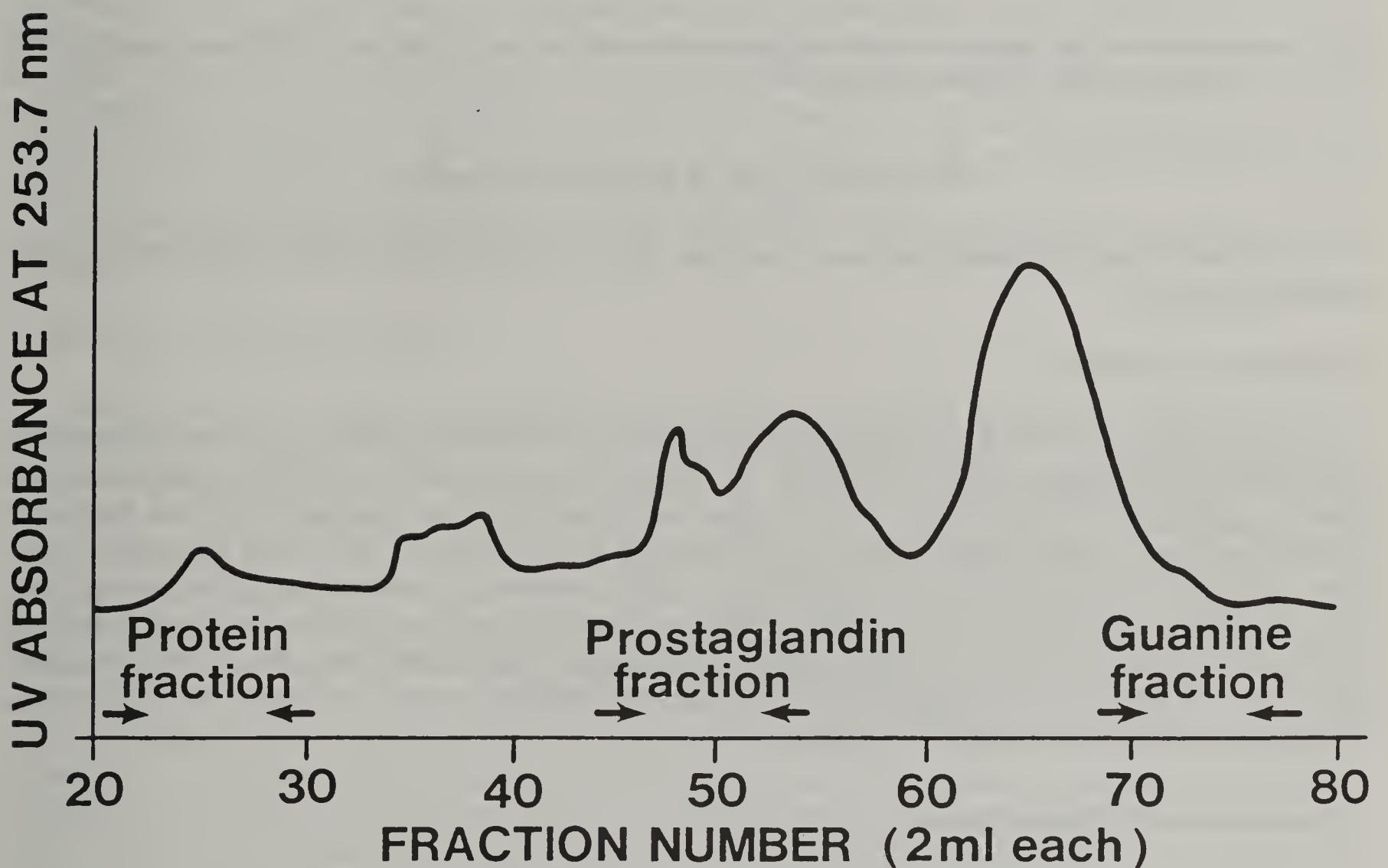


Fig. 3. –Gel filtration on LH 20 Sephadex of saliva obtained by pilocarpine stimulation from adult female ticks.

Morphology of the Salivary Gland

Histological studies have revealed that the salivary gland of *B. microplus* (see Fig. 4) contains three acini, one of which is agranular and presumed to function in osmoregulation; the two granular acini contain a total of nine cell types of which three function in the production of attachment

cement precursors, the remainder producing granules rich in mucoproteins and enzymes – a non-specific esterase, acetylcholine esterase, phosphatase and protease – the significance of which is unknown (Binnington, K.C., personal communication).

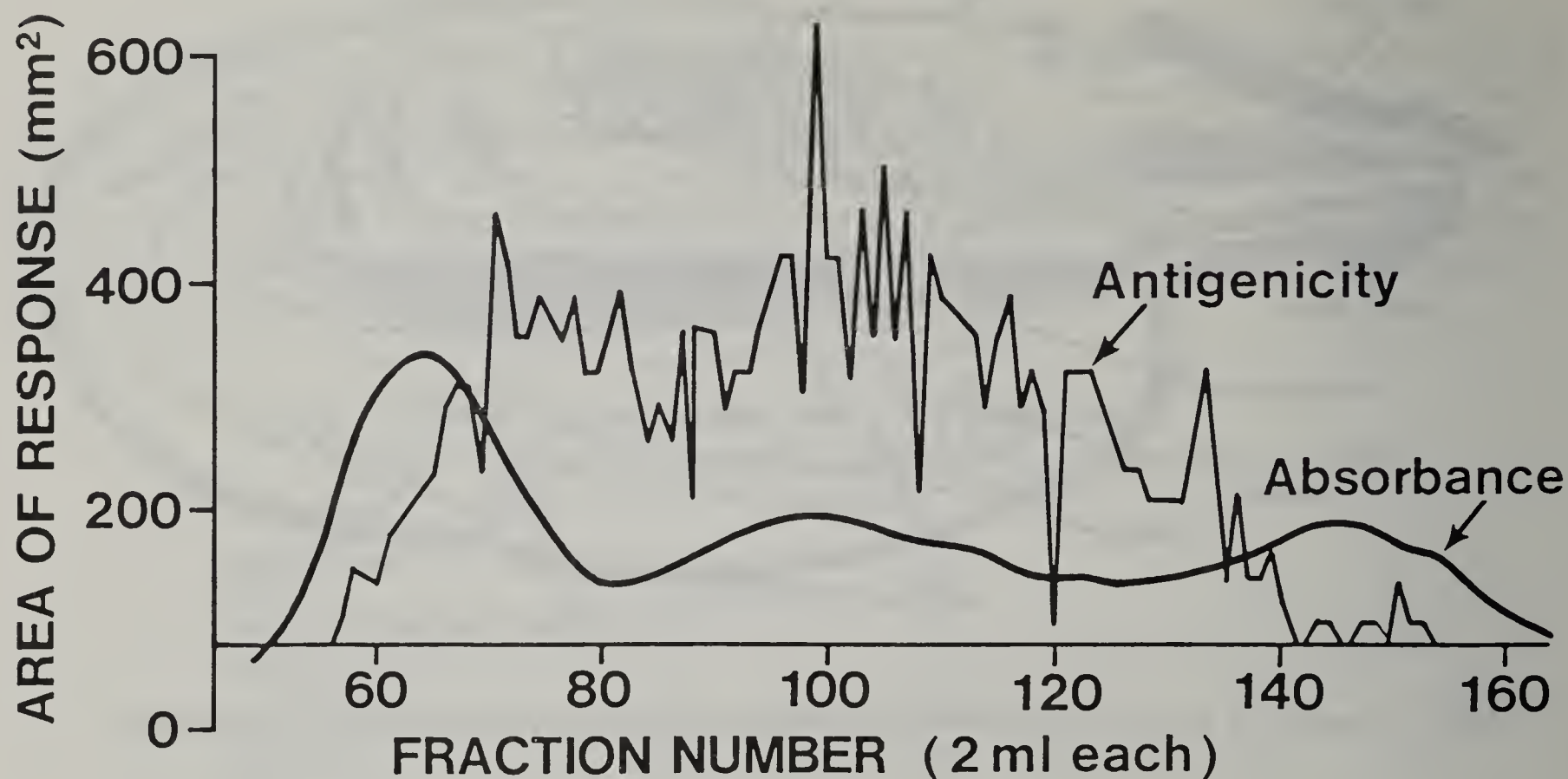


Fig. 4. –Fractions from gel filtration in saline of protein fraction from LH20 Sephadex separation tested for ACA activity in the skin of a previously exposed bovine.

The Oral Secretion of the Salivary Glands

The tick's salivary glands perform a number of functions some of which assist feeding and survival of the tick.

1. Secretion of Cement

The cement cone has been described by Moorhouse and Tatchell (1966) as having a “cortex of carbohydrate-containing protein, stabilized by quinone tanning and disulphide linkages and an internum which is lipoprotein in nature.” This description may be oversimplified and the cone material has been found to have many constituents but the presence of muco- and lipoproteins has been confirmed by electrophoretic analysis (Stone, B.F., personal communication). The cement may not only relieve some ticks of the necessity to hold on firmly by their tarsi during their long period of attachment. In the case of *B. microplus* which has relatively short mouthparts the cement may also secure the tick to the host during the critical period of moulting to the next instar. At this time the holding strength of the tarsi might be low.

2. Development of Feeding Lesion

While the exact contribution of the saliva to the formation of the feeding lesion below the mouthparts has, as yet, not been clearly defined, it can be stated that the lesion may not be absolutely necessary for tick survival. Thus Tatchell and Moorhouse (1970) prevented the formation of the lesion caused by *Rhipicephalus sanguineus* (Latreille) by injecting dogs with nitrogen mustard to destroy leucocytes. The ticks fed and laid eggs giving viable larvae. The saliva does however contain a number of enzymes, notably esterases, acid phosphatases and a carbohydrate-splitting enzyme (Tatchell 1971, Geczy et al. 1971). In the skin of previously unexposed calves, 4 hr after infestation at the site of attachment of larvae, three esterases, a lipase, a peptidase and a phenoloxidase were detected, presumably coming from larval saliva (Schleger, A.V. and Lincoln, D.T., personal

communication). These enzymes may help to destroy membrane barriers to the flow of nutrients and so increase vascular permeability. No anticoagulins have been detected in *B. microplus* (Tatchell and Binnington 1971) nor has infestation been found to alter significantly the concentration of the host's blood coagulation factors (O'Hagan, unpublished). Likewise Barker (Characterization of oral secretion and salivary gland homogenate extracts of *Amblyomma americanum* (L.) Acarina: Ixodidae, Ph.D. Thesis, Oklahoma State University 1973) found no haemolytic activity in salivary gland homogenates, but on the other hand *Ornithodoros moubata* (Murray) was found by Hellmann and Hawkins (1967) to have an antithrombin in salivary glands, gut, eggs and coxal fluid.

3. Elimination of Water, Salts and Waste Products

Water removal allows concentration of the blood meal and thus more food to be imbibed and stored (Tatchell 1967, 1969, Kitaoka and Morii 1970). Amino acids are also present in adult female saliva (Tatchell 1969) in relatively large amounts and these may represent the elimination of material unwanted for the synthesis of tick proteins or utilization as food, it being too much to expect that cattle blood would be a perfect diet. While hematin is probably too insoluble to be removed and has not been found, I will describe later the finding of guanine in adult female saliva. Thus the salivary gland would appear to act like the mammalian kidney in eliminating waste products of metabolism.

4. Secretion of Pharmacologically-active Substances

Feeding may be assisted by the secretion of substances which increase capillary permeability (Tatchell and Binnington 1971) and so promote the movement of blood and tissue constituents into the region of the mouthparts. A complement-derived chemotactic factor has been found by Berenberg et al. (1972) to be formed when the extracts of the salivary glands of *Dermacentor variabilis* (Say) were added to human or dog serum. No activity was found without the serum. Neutrophils were attracted by the factor and the authors ascribed the destructive effect in tick-bite injury to the presence of these host blood cells. Further work on pharmacologically-active components of tick saliva will be described later in this paper.

As well as these functions which would favour the tick survival the gland performs others which would seem to be not in the tick's best interests.

5. Secretion of Toxic Substances

While the toxic effects of saliva from *B. microplus* are difficult to prove, O'Kelly and Seifert (1970), O'Kelly et al. 1971, Seebeck et al. (1971) and Springell et al. (1971) consider the anorexic effect of tick infestation to be due, at least in part, to a toxin. There is weight loss, disturbance of protein and lipid metabolism suggestive of liver dysfunction. The effects of *B. microplus* in this respect are very mild when compared with other toxin-producing ticks such as *Ixodes holocyclus* (Stanbury and Huych 1945, Doube 1975, Doube and Kemp 1975, Doube, Kemp and Bird 1976) which can paralyse and kill young unexposed calves when 10 ticks attach. The toxin is found in the glands of ticks that have fed for several days and has been partially purified by Kaire (1966). Recent studies indicate that the toxin is a low molecular weight protein (Doube, B.M. and Nolan, J., personal communication). Extensive studies have been reported by Gregson (1973) of similar effects caused by *Dermacentor andersoni* (Stiles) producing dysfunction at the neuromuscular junction and a toxin of protein nature has been purified by Neitz et al. (1969) from *Ornithodoros savignii*. The exact nature of the toxins involved and their possible significance for tick survival awaits further study but Nelson et al. (1975) have suggested that the toxins may have value for ticks in that they inhibit host grooming, though if the host dies it would be disadvantageous.

This emphasises the perfect balance required between parasite and host remarked upon by Mahr (1957), "If the parasite becomes too successful it will kill the host, and if the host becomes too successful it will eliminate the parasite."

6. Secretion of Antigens

Saliva contains antigenic substances (identical perhaps with those discussed under 2. and 5. above) which when injected into the skin of previously exposed hosts produce active cutaneous

anaphylaxis. This is brought about by the discharge of mast cells in the host skin, which does not occur with unexposed hosts and is significantly greater with highly resistant hosts. (Schleger, A.V., Lincoln, D.T., McKenna, R.V., Kemp, D.H. and Roberts, J.A., personal communication). Mast cell degranulation results in the release of histamine and the injection of a very small quantity of histamine ($3\mu\text{g}$) in vivo beneath the mouthparts causes a high proportion of larvae to detach (Kemp, D.H. personal communication). With larvae on hosts of high resistance initial growth rate of larvae was slower, attachment times were shorter and more wandering occurred (Kemp et al. 1976).

Antigens also release eosinophil chemotactic factor of anaphylaxis (Orange et al. 1970, Kay et al. 1971) and this could explain the marked infiltration of eosinophils into the area below the tick mouthparts on previously exposed hosts found by Tatchell and Moorhouse (1968).

The development of homocytotropic antibodies would appear to play an important part in host resistance to the tick and personal researches in this respect are described later.

Biochemical Studies on Tick Saliva

Analyses of tick saliva were long hampered by the small quantities available and the tediousness of techniques of collection. This has been overcome, at least for the cattle tick, by the development by my colleagues Binnington and Schotz (1973) of a method for the collection of saliva from 1300 adult female cattle ticks per day using a modified fraction collector. With this method about 12 ml can be collected per run, frozen, pooled and freeze-dried so that over four months the product represents the output of 120,000 ticks or 1 litre of saliva. We have done this several times and fractionated the product as follows.

The protein fractions, which appear first, contain the antigens to which previously-exposed hosts are sensitive (O'Hagan and Schotz 1976). Not only have we found these antigens in the saliva, but also in haemolymph, salivary glands, larvae and eggs and Willadsen and Williams (1976) have isolated and partly characterised a larval esterase with high antigenicity. Although our work on saliva has been with ticks which have completed their parasitic life, it would appear from these findings that it may be applicable to saliva of other instars. The findings may have significance in another field in that in assessing the effects of the house dust mite, *Dermatophagoides pteronyssinus* (Trouessart), in relation to human asthma (Maunsell et al. 1968) the possible contribution of eggs and instars other than adults (which in practice are the only stages counted) should be taken into account. Counting the adults may not give a true picture of the antigen stimulus by a rapidly growing population of mites.

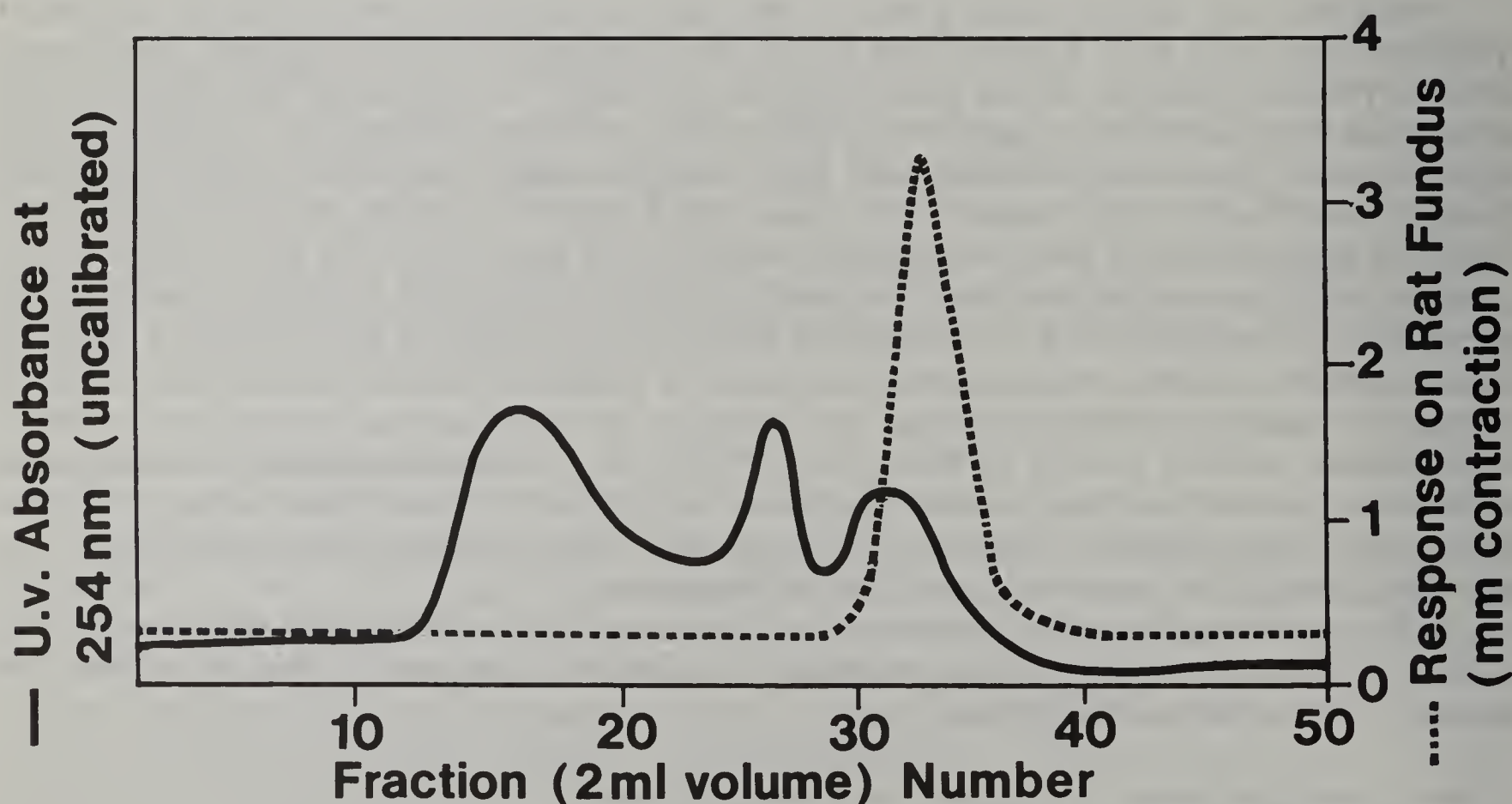


Fig. 5. —Response of rat fundus to fractions from CM C25 Sephadex gel filtration of pharmacologically-active fraction from LH20 Sephadex filtration.

The next group of fractions appear to contain peptides, followed by fractions containing aminoacids and smaller molecules. The last fraction has been found by U.V. analysis to contain guanine, an end product of nitrogen metabolism in the tick.

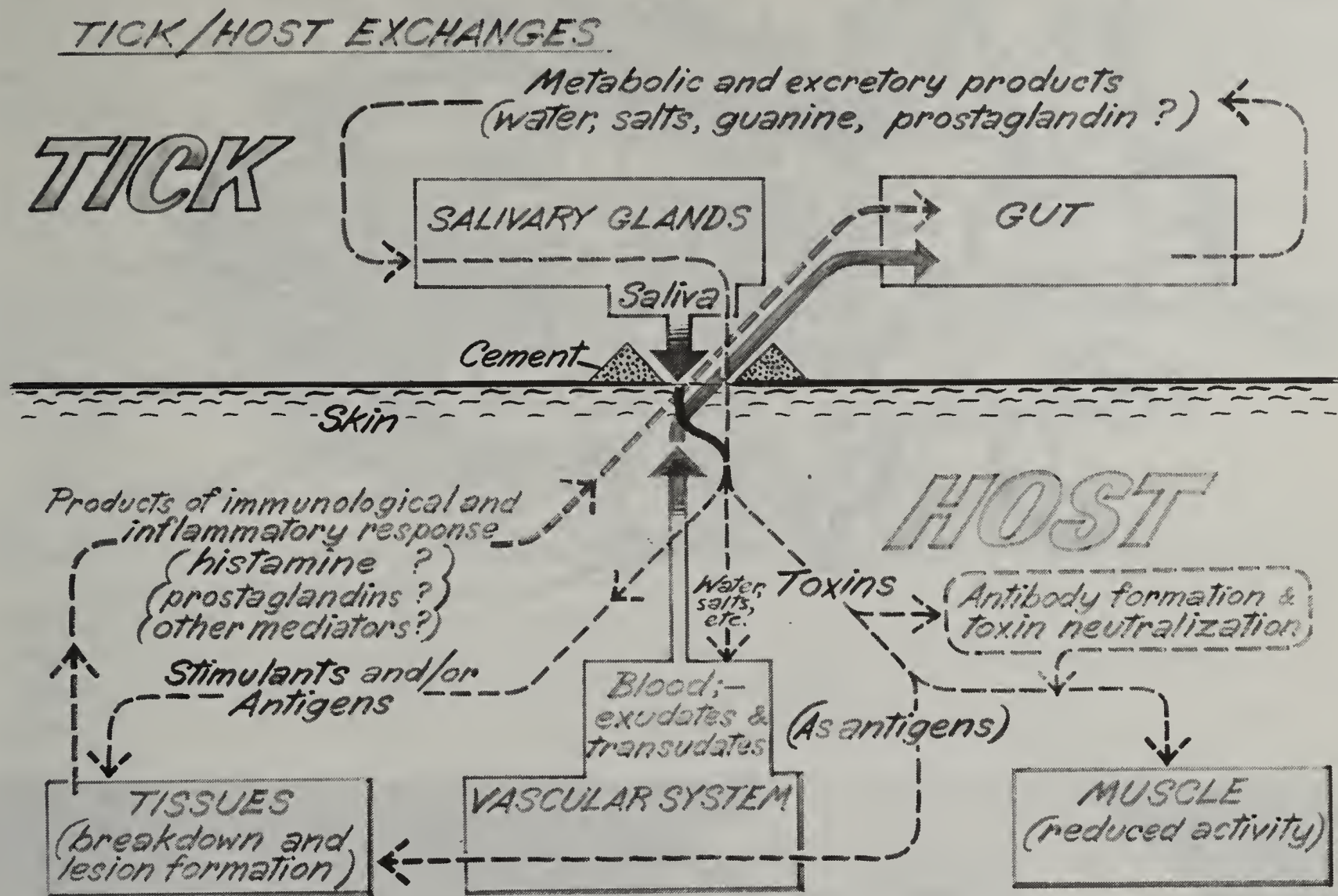


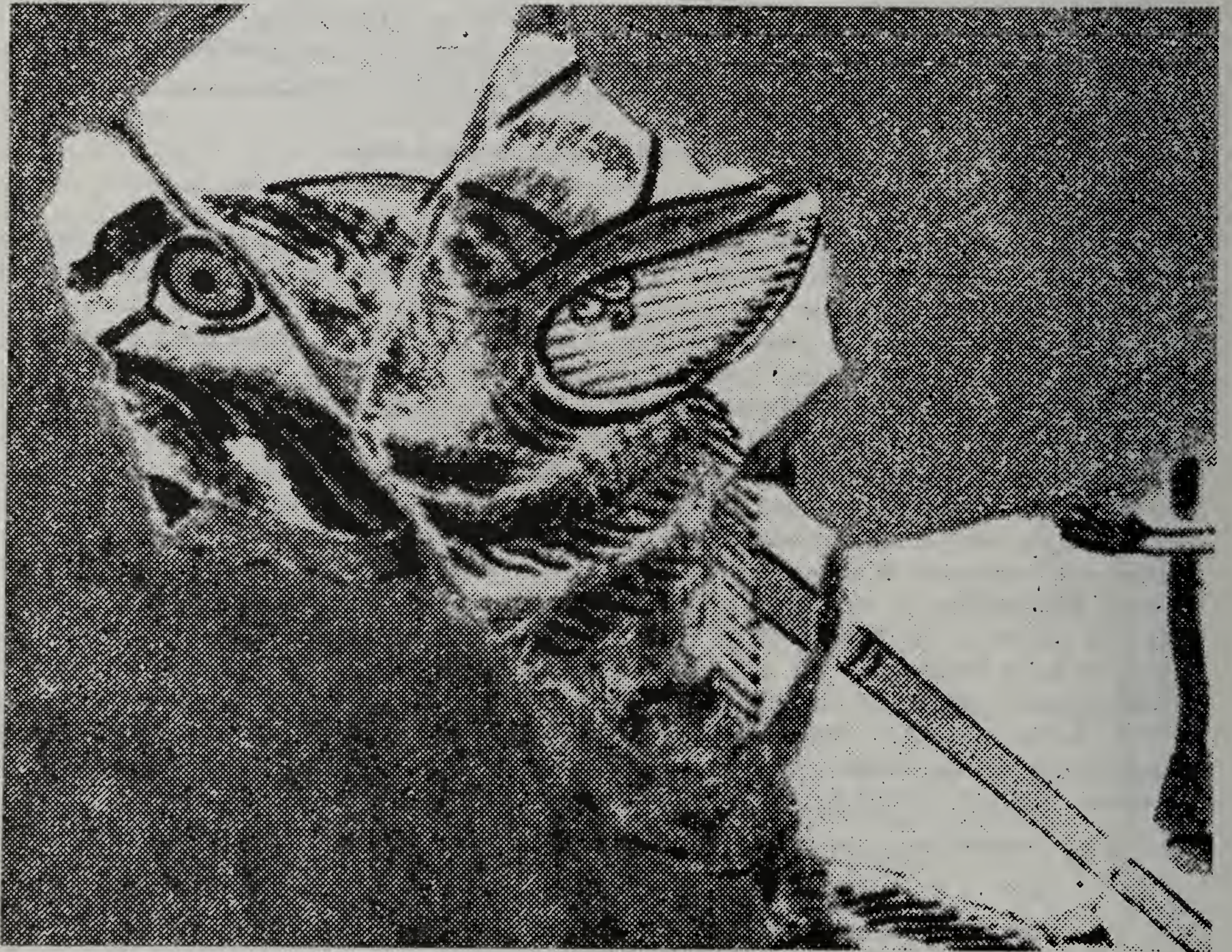
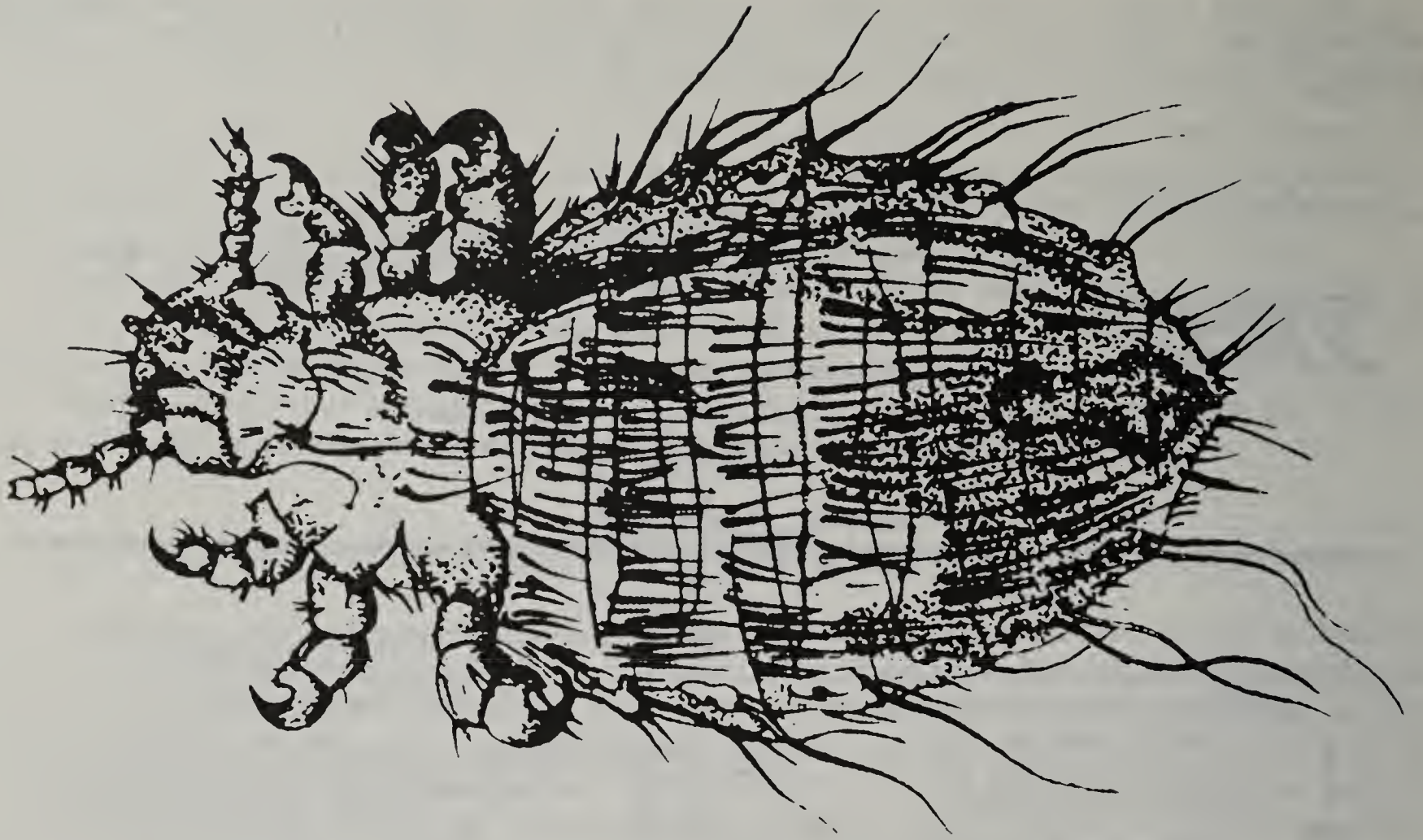
Fig. 6. –Diagram summarizing tick host exchanges.

In the peptide fraction a pharmacologically-active substance giving contractions of isolated smooth muscle preparations has been detected and in the amino acid fraction a prostaglandin with the characteristics of PGE_2 has been isolated (R.G. Dickinson, J.E. O'Hagan, M. Schotz, K.C. Binnington and M.P. Hegarty, in press; G.A. Higgs, J.R. Vane, R.J. Hart, C. Potter and R.G. Wilson, in press). This corresponds with the "active constituent" first detected by Tatchell and Binnington (1971) and studied further by O'Hagan et al. (1973). While a prostaglandin has been found previously in an arthropod by Destaphno et al. (1974) in the reproductive tract of a male house cricket *Acheta domesticus* (L.), this is the first time such a substance has been found in the vicinity of a host-parasite interaction. Prostaglandins E, A and B have been found to cause the expulsion of adult worms of *Nippostrongylus brasiliensis* (Travassos) from the small intestine of the rat (Dineen et al. 1974). Our findings could represent an attempt by the host's cells to dislodge the parasite, it could be the result of tissue inflammation (a condition resulting in the appearance of prostaglandins in the exudates therefrom (Zurier 1974, Kurti et al. 1974)), or could have been a normal host blood component, capable of being returned by the tick, either as an excretory product, or for its own purpose of increasing host capillary permeability, or be produced by the tick for the same purpose. The answer to this question requires further work, but it is interesting that Higgs et al. (1975) found phagocytosing polymorphonuclear leucocytes, known to produce the feeding lesion (Tatchell and Moorhouse 1970), excrete up to ten times as much prostaglandin as do resting cells.

Conclusion

We can sum up the situation diagrammatically as shown in Fig. 8.

The tick secretes cement for attachment and injects other components of the saliva into the host, stimulating the production of a feeding lesion. The host response provides exudates and transudates, followed eventually by whole blood. The tick returns water, salts and small molecules



such as prostaglandin which may or may not have been originally derived from the host, and guanine, an end product of nitrogen metabolism. Proteins, most probably secreted by the tick to assist feeding, act either as antigens producing varying degrees of resistance to tick attachment by the host or as toxins again affecting the host in varying degrees. More knowledge of the physiology and biochemistry of the interrelationships would give a better understanding of the processes involved as well as leading perhaps to the development of new methods of tick control. One could speculate that usage of such methods could enable us to participate in changing the path of the evolution of the relationship between arachnids and their hosts.

Acknowledgment

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Physiology and Biochemistry of Insect Host Interactions: Conclusions

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When I try to summarize the ideas of the various speakers of this morning's session, some points deserve, I think, special attention. The first point is related to the question: which aspects of insect-host interactions do we understand more or less, and where is our knowledge? A second point of interest which I may bring up concerns the mechanisms involved in insect-plant interactions in comparison to those in insect-animal relationships.

Insect-plant relations are to a large extent based on chemical cues, as almost unanimously is agreed upon as we heard this morning from Dr. Städler. However, the original idea that simple token stimuli, one or a few characteristic chemicals, are representative for a given food plant is too simplistic and instead, as Dr. Kogan has rightly stated, the insect obtains a fairly complex chemical image of its food, a Gestalt. Probably because of this only a few insect-plant relationships are well understood, due to our very limited knowledge of the plant's chemical composition and of its variations in space and time. I think much more information is needed in this respect and cooperative efforts of plant physiologists and entomologists could lead to important new discoveries.

In insect-animal relationships the aspect of host selection is somewhat different. Here the role of visual and temperature stimuli are often important, which is due to the fact that animal hosts are mobile beings. However, also here chemical signals are essential and Dr. Galun has indicated that often olfactory signals override other cues. The importance of chemical factors in an insect host-parasite relation is beyond doubt. Again like in the insect-plant system, our information on animal host odors is scarce. Analysis of such odors has begun only recently and when more information over this becomes available we may expect to gain a better understanding of host recognition. In addition, when in the near future we know more of the inter-individual variations in odor composition the differences between host individuals in attractivity for parasites will probably become clear.

The title of this symposium includes the term relationships, which means that we are interested not only in the insect but in the whole insect-host system, including the responses of the host. It seems to me that in this respect there are striking differences in our knowledge of animal hosts in comparison to plant hosts.

In vertebrates immune responses and skin reactions counteract the insect parasite, as has been discussed by Dr. O'Hagan and Dr. Galun. In insect hosts, parasitoids may be encapsulated by blood cells. Thus immediate and strong defense reactions are known to occur in animals. Our knowledge on long-term reactions, however is scanty.

In contrast we know little about short-term physiological reactions in plants, although some investigations on changes in crop yield after insect attack, or changes of chemical composition of plants and gall formation as a reaction to insects indicate the existence of physiological reactions. This seems a neglected, but promising field of research. There is strong evidence for long-term effects which insects have induced in plants and Dr. Swain has elaborated on the plant defense systems which were developed during evolution. Extensive breeding programs for insect resistance are based on the existence of such defense systems.

In conclusion it may be said that insects and their hosts, be it plants or animals, show intricate relationships, in which many factors act together. It seems likely that the stability of such relationships is a result of this complexity.

Section 6: Behavior

Pheromones, Allomones, and Kairomones: Their Significance in Insect Biology

Organizer: Murray S. Blum (USA)

Moderator: Jacques M. Pasteels (Belgium)

Evolutionary Aspects in Chemical Ecology and Chemical Communication

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Introduction

The concept of *pheromones* (Karlson and Lüscher 1959), and hence those of *allomones* and *kairomones* which arose from the former (Brown et al. 1970), seem to be the outcome of a functional analogy between organisms and pluri-individual systems. This analogy is indicated explicitly by several synonyms: (Bethe, 1932), external diffusing hormones (Huxley, 1935); sociohormones (Grasse, 1954), or environmental hormones (Odum, 1971).

Like hormones, pheromones, allomones and kairomones are chemicals which function as regulators or instructions leading to specific development, structures and processes, acting as anti-entropy agents, but at the level of populations, societies and communities. Often their functions can be schematized as simple negative feedback loops, or as parts of more complex ones (Fig. 1). The study of such chemical interactions is one of the main topics of "chemical ecology".

In an attempt to investigate the extent of our present understanding of these mechanisms, I will consider those evolutionary trends which may be deduced or suspected from comparative studies carried out at both the species and the community levels.

Some definitions and concepts will first be briefly discussed.

Ecomones: Pheromones and Allomones

Signals and regulators within pluri-individual systems are most frequently divided into three main categories : pheromones, allomones and kairomones. This classification does not, however, seem satisfactory. The distinction made by Brown et al. (1970) between allomones and kairomones according to whether the adaptative value falls upon the emitter or the perceiver has already been criticized (Blum, 1974a, Pasteels, 1973). Blum (1974a) considers that kairomones "appear to be pheromones and allomones which have evolutionarily backfired" and that they "do not represent a class of chemical signals distinct from allomones and pheromones." Moreover, the distinction between adaptative and inadaptative is not always evident. A signal which seems inadaptative at the individual level, might be adaptative at the population level; this will be discussed in more detail later. Chemicals emitted outside the organisms may have several functions. Adaptative value must be evaluated by taking into account all these functions. As a matter of fact, a truly inadaptative compound is necessarily transitory, and will be eliminated by selection. For these reasons it seems premature to consider kairomones as a major category. The term "allomone" will be used for all transspecific messengers, of which kairomones could be one of the several possible subcategories indicating one particular aspect of the interaction. This is to be preferred to the term "allelochemic" (Whittaker and Feeny, 1971) as definitely more euphonic.

Several important chemical signals do not fall easily into these categories. For some species of *Culex*, suitable oviposition sites are located due to attractants and arrestants emanating from water

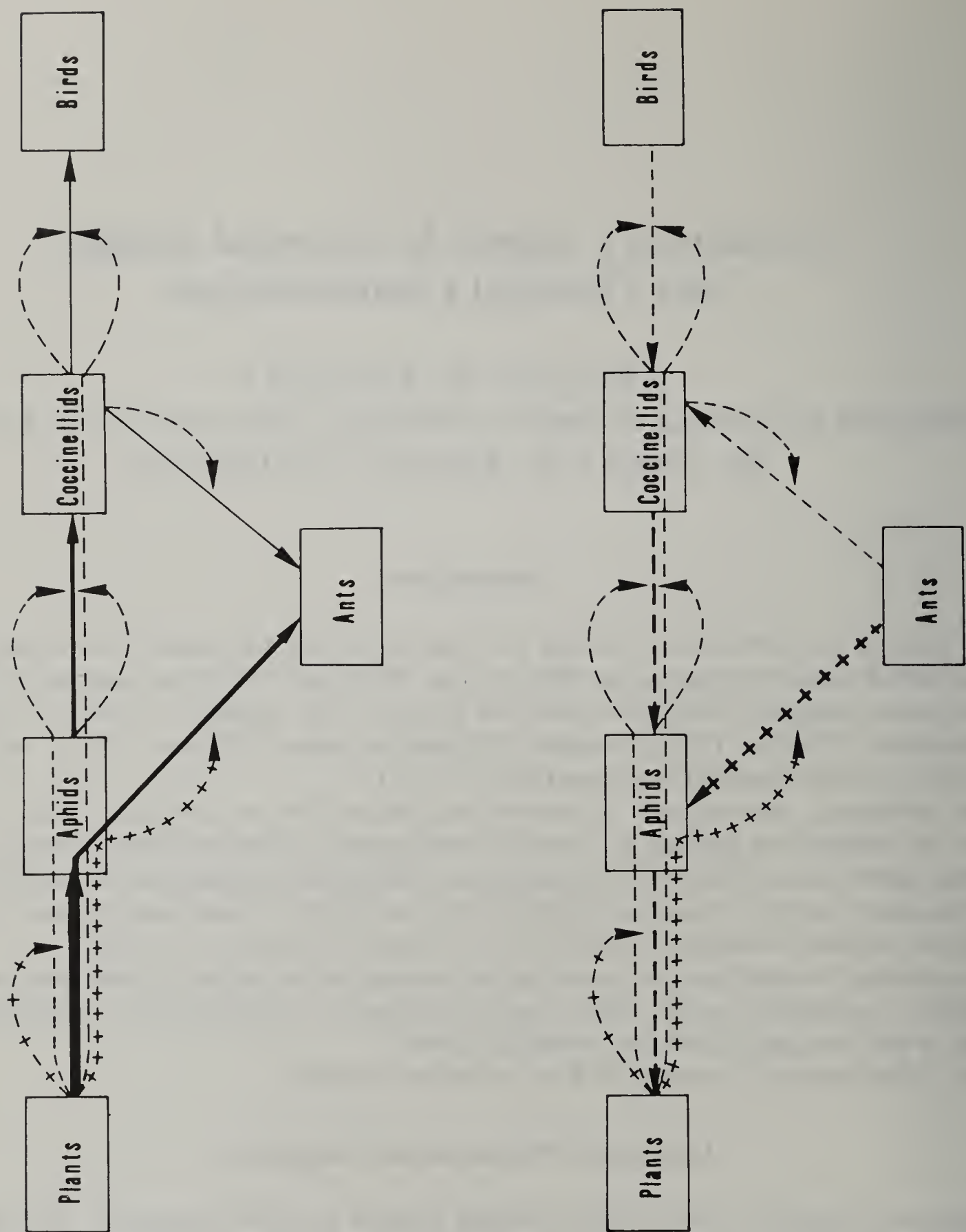


Fig. 1. —Allomonal regulation in a simplified food-web. The arrows ending with a loop designate allomone effects (+ or -). Above, the energy flow between trophic levels is represented by straight arrows. Allomones appear as “sluice-gates” which regulate this flow.

Below, the straight arrows indicate the effects (+ or -) of a trophic level on the preceding one. Allomone effects appear as feedback loops, either positive or negative, favoring mutualistic relationships (+,+) or predatory relationships (+,-), or acting as protective devices (-,-).

All these allomone effects and transfers have actually been recognized in specific food chains involving species belonging to the groups considered here: food plant is sometimes recognized by aphids after probing it with the rostrum (Kennedy and Fosbrooke, 1972) and allomones must play a key role in this choice; *Aphis nerii* eating on *Cionura erecta* (Asclepiadaceae) accumulate toxins which affect the development of *Adonia variegata* (Pasteels, unpublished), cornicle secretions are effective against ladybirds (Edwards 1966); *Coccinella 11-punctata* accumulates cardenolides originating from oleander via *Aphis nerii* (Rothschild 1972); the honeydew produced by aphids contains unmodified plant sap compounds such as sugars acting as phagostimulants for the ants (Way 1963); many coccinellids synthesize alkaloids repulsive to ants and birds (Pasteels et al. 1973).

rich in decaying organic matter (Ikeshoji, 1966). Many decomposers are attracted by specific compounds produced during decay processes. Are the senders of these signals the bacteria or the various living organisms, which gave rise to the dead organic material? The question is without any real interest. It is even conceivable that dead material and signals are imported from outside the community. What is of real importance is that such signals trigger some specific process within some particular environment, which is in fact the real sender of the signal. This is particularly obvious for the chemicals which guide salmon to their natal stream (Scholz et al. 1976).

Thus we need a very general term in order to designate compounds that act as signals or regulators and originate either from organisms or from the abiotic environment. The very suggestive word *ecomone* coined by Florkin (1965) (see also Florkin and Schoffeniels 1969 or Pasteels 1973) seems most appropriate for that purpose.

Evolutionary Aspects

It is a straightforward matter to propose certain general evolutionary trends for each species taken separately. Trends are far more difficult to formulate when the community is considered as a whole.

At the species level, evolution must be towards an increase in the efficiency of the produced ecomones, without too great an increase in the cost of their production. Economy in biosynthesis and releasing mechanisms, and increase in efficiency will be successively discussed.

Economy principle

The production of ecomones, most of them being rather unusual compounds, is certainly a costly metabolic process when we consider the complex glandular machinery needed for their biosynthesis, and their efficient release, as well as self-protection mechanisms against toxic chemicals. Several examples are known of mechanisms which limit this cost. In extreme cases, ecomone production stops if substitute alternatives become available: ant-acacias appear to have lost the chemical defences of non-ant acacias (Rehr et al. 1973).

Economy in glandular equipment. — The same exocrine gland is sometimes used for completely different purposes in the same individual, or according to the life stage of the insect. In primitive termites such as *Zootermopsis*, the sternal gland of nymphs secretes the trail pheromone (Lüscher and Müller 1960, Stuart 1963). In swarming adults, it produces sex-specific pheromones (Pasteels, 1971). The pheromones are different as proved by bioassays but they may be closely related. In fact, the closer the chemical relation, the greater would be the economy.

Also, when different pheromones are secreted by the same gland, but in different castes, as is frequently observed in social insects, there is an economy at the level of the genetic equipment common to all castes. Again the economy will be greater if the pheromones are more closely chemically related or even identical as suggested for trail and sex pheromones in some ants (Hölldobler, 1971b), and in *Trinervitermes bettonianus* (Leuthold and Lüscher, 1974).

Multifunctional compounds. — It is a well-known fact that a single compound may have several meanings. Various defense compounds are used as alarm pheromones in both social and subsocial insects (reviews in Blum, 1974b, c). Moreover ethologists are well aware of the fact that the meaning of a signal is a function of the context in which it is released, of its intensity and of the target individuals. This is nicely illustrated in many social insects where pheromones may have very different meanings when emitted inside or outside the nest, and according to concentrations or target castes. This multiple use of the same pheromone was called “pheromonal parsimony” by Blum (1970) who reviewed the subject. The most striking example remains the very versatile function of 9-oxo-decenoic acid in domestic bees (Butler, 1969).

It must be stressed that evolution towards the multiple use of the same gland or the use of multifunctional compounds is to be expected in chemical communication “sensu stricto.” The evolution of chemical communication has arisen most probably by a process similar to ritualisation. During the course of evolution, the selection of individuals which do respond to a compound as a signal cannot precede the actual emission of that compound. Signals must thus evolve from preexisting secretion. Some of them could already act as pheromones in other contexts. As a matter of fact, in this latter case, the sense organs would already be preadapted.

Use of chemicals sequestered from food. — Many insects sequester secondary substances from their food plant and use them as defense compounds and sometimes as pheromones.

How far sex pheromones may be diet related is still a controversial question (Miller et al. 1976, Hendry 1976).

The storage of plant defense compounds in insects is much better documented and has been studied in great detail in the monarch butterfly (Brower and Glazier 1975). It is obviously an economy for the insects, since detoxifying and excretory mechanisms are combined with chemical defense. Rothschild (1972), published a list of 43 species from six different orders which sequester and store plant toxins. Three of them are secondary consumers: *Coccinella undecimpunctate*, larvae of *Chrysopa* sp. and a Tachinid, *Zenilla adamsoni*. The variety of stored compounds known is already large, and will certainly increase: aristolochic acids, cardenolides, alkaloids, mustard glycosides, hypericin, and terpenes (ref. in Rothschild 1972, Eisner et al. 1974). This frequent use of plant toxins is even more significant in that insects themselves are remarkable chemists, with performances not very far below those of plants. Coccinellids synthesize their own alkaloids. Incorporation experiments with radioactive acetates demonstrate that coccinelline can be biosynthesized through the polyacetate pathway (Tursch et al. 1975). Pederin is synthesized by some staphylinids (Cardani et al. 1973) and cantharidin by meloids. A remarkable study of the biosynthesis of cantharidin in the spanish fly (*Lytta vesicatoria*) has recently been made by Sierra et al. (1976). Only the males biosynthesize cantharidin from terpenoid precursors. Copulation greatly increases the biosynthesis. Cantharidin is stored in the male accessory glands, transferred to the females during copulation, and subsequently accumulates in her eggs.

Together with D. Daloze, we have recently reached the conclusion that some chrysomelids are able to synthesize cardiac glycosides from unknown precursors (Pasteels and Daloze, unpublished). Cardenolides were detected in the secretion of the prothoracic and elytral defense glands in 9 species out of 20 checked. All the species in which cardenolides were found belong to the genus *Chrysolina* and two related genera *Dlochrysa* and *Chrysochloa*. These species feed on plants belonging to three different families: Labiatae, Compositae, and Scrofulariaceae, each insect species being a specialist on one or a few of them. Cardenolides have been described in none of the host plants, some of which are even used in cookery, like peppermint or rosemary.

Cardenolides can be easily detected by milking the defensive secretion of a single individual of *Chrysolina coerulans*, whereas they could not be detected in almost one Kg (fresh weight) of leaves of *Mentha* sp. (on which they were bred), an amount of food plant large enough for breeding several hundreds of beetles. The same experiment was repeated with the same result using *Rosemarinus officinalis*, host plant of *Chrysolina americana*, and *Galeopsis tetrahit*, host plant of *Dlochrysa fastuosa*.

It is tempting to speculate that some insects could lose their ability to biosynthesize complex defensive compounds when the storage of plant toxins becomes available. This would be a shift towards a more economical defensive strategy. This could happen when an already well protected insect species moves from non toxic plants to a new highly toxic host plant. No clear example of such evolution is known, but this could be due to our present lack of understanding of the evolution of insect defensive strategies.

So far the only *Chrysolina* species found to be devoid of Cardenolides live on *Hypericum*. This is a striking result since at least some of them are known to store hypericin (Rees 1969). This could be an example of a shift towards a more economical defensive mechanism. It is however as easy to speculate that *Hypericum* lacks the right precursors for the synthesis of Cardenolides by the insects, or that the absence of the enzymes needed for such synthesis is a primitive condition in these species. More experiments, including incorporation experiments with labelled compounds, are needed to establish which precursors are used by the insects.

From Müllerian to Batesian mimicry. — Batesian mimicry is well documented in insects and needs no further development here (Brower et al. 1975, Rettenmeyer, 1970, Rothschild et al. 1973, and references therein). It is of course one way of avoiding the load of chemical defense. I would just like to draw attention to the possibility that Batesian mimicry might sometimes evolve from Müllerian mimicry.

We have recently found such a possible evolution in sawfly larvae (Pasteels, Braekman, Gregoire and Araujo, unpublished). When disturbed, the easily noticeable larvae of *Nematus melanopsis* secrete copious amounts of benzaldehyde and 2-heptenal from a row of unpaired ventral glands. In the less common sympatric species, *Nematus saliceti*, the glands seem to have lost their defensive function.

They are small, odourless, and very difficult to force to evaginate. The larvae of the two species are aposematic and look similar at first sight, but the efficiency of the postulated mimicry awaits experimental proof.

Conclusion

It is thus possible to recognize several mechanisms which do limit the cost of ecomone production. Some of these mechanisms like the use of multifunctional compounds or the multiple use of the same gland seem to be the result of an evolution similar to ritualisation, i.e. the selection of individuals responding in an appropriate way to an already existing compound and a progressive increase in the efficiency of emission according to the new signalling function of the compound. In these cases, economy seems to be more a happy consequence than a prime mover of evolution.

We cannot exclude however that economy has been a significant mover during the evolution of some defensive strategies even if the evidences for such are still dim. Defense can be achieved in many various ways: the cheapest would be the best.

Increasing the efficiency

Besides economy, a second general evolutionary trend must of course be an improvement in the efficiency of chemical communication and control. This will be discussed first for pheromones.

Pheromones. — The most obvious increase in efficiency has been a better tuning of the chemoreceptors for the detection of pheromones, as demonstrated by the occurrence of pheromone specialists besides generalists among the chemoreceptors of insects (Schneider, 1969).

Other evolutionary trends can be deduced from the theoretical work of Wilson and Bossert (1963).

Wilson and Bossert have compared general characteristics of pheromone communication, such as size and complexity of the molecules (related to specificity), active space around the source, and fade-out time. These characteristics must differ according to the functions of the pheromones such as alarm, trail or sex pheromones, so that predictions can be made about the optimal ranges of molecular weights, quantities of pheromone released and threshold concentrations.

Recent comparative studies of chemical communication clearly indicate that efficiency may be increased during evolution by a progressive adjusting of fade-out time and active space, or by narrowing the specificity of the signals.

Comparative studies on the sex pheromones of Tortricids and Noctuids strongly suggest that sex attraction has evolved towards a more and more narrow specificity by the addition of inhibitors or synergists in fixed proportions, by the tuning of the emission and the perception of pheromone to a restricted concentration range, or by diversifying the moments within a circadian cycle when communication occurs (review by Roelofs and Carde, 1974).

Progressive adjusting of the active space and fade-out time of pheromones seems to have occurred during the evolution of recruitment mechanisms in ants. Food, nest-moving or defensive recruitments are the result of three kinds of signals: orientation signals layed when a recruiting ant returns home, alerting signals performed in or near the nest and leading signals released when a recruiting ant guides the recruits (Maschwitz 1975, Pasteels 1975).

The active space of the orientation signal, layed as a trail, must be narrow, and its fade-out time rather long; whereas the alerting signal must have a rather large active space, but shorter fade-out time. The leading signal should have intermediate characteristics.

Three main recruitment methods have already been recognized, which may represent successive evolutionary stages: tandem, group and mass recruitments (review in Maschwitz 1975).

During tandem recruitment, the chemical leading signals are either absent, or are surface contact pheromones (e.g. *Bothroponera tesserinoda*, Maschwitz et al. 1974, *Camponotus sericeus*, Möglich et al. 1975) or are pheromones secreted by the poison gland, but effective only at a short distance (e.g. several *Leptothorax*, Möglich et al. 1974). Recruited ants are led one by one. When present, leading and orientation signals are always distinct. Alert is usually the result of a particular invitation behavior performed in the nest and is purely mechanical, except in *Leptothorax* in which the leading signal has an alerting effect.

In group recruitment, the active space of the leading signal is larger but its fade-out time short: a few ants are led at short distances by the leader (e.g. *Camponotus socius*, Hölldobler, 1971,

Myrmica rubra Abraham 1976, *Tetramorium caespitum*, Verhaeghe, 1975, *Megaponera foetans*, Fletcher 1973).

Only two such pheromones have been identified yet. The leading signal in *Camponotus socius* is formic acid produced by the poison gland (Hölldobler, 1971). In *Myrmica rubra*, it is a complex mixture released by the Dufour's gland at least during defensive recruitment (Cammaerts-Tricot 1974). Acetaldehyde is the most potent attractant of the Dufour's gland pheromone in this species (Cammaerts-Tricot et al. 1976). Such pheromones are fairly volatile, and certainly different from the orientation signals produced from other sources: the poison gland in *M. rubra*, and the hind gut in *C. socius*. The leading signal has an alerting effect, but the mechanical invitation behavior is still important.

In mass recruitment there is a very precise adjustment of active space and fade-out time, so that the same pheromone acts as orientation, leading and alerting signals (*Solenopsis saevissima*, Wilson 1962a, *Lasius fulliginosus*, Maschwitz 1975). The active space is large enough to attract workers at some distance, but without greatly impairing the precision of the trail. Fade-out time is such that the trail will remain only if it is continually reinforced by recruiters. Very precise recruitment in time and space can be achieved by this highly evolved mechanism.

All three evolutionary stages are known in both Formicinae and Myrmicinae and at least tandem and group recruitment, in Ponerinae.

Thus thanks to a few detailed comparative studies, we are beginning to understand how some communication by pheromones has evolved or could evolve.

Allomones. — The evolution of allomonal control towards an increase in efficiency is in some cases easy to understand.

At least some pollinization allomones, such as orchid fragrance (Dodson, 1973), have evolved towards an increasing specificity. Indeed pollinization allomone communication has parallels with that of sex pheromones.

Also the perception of allomones like food attractants or phagostimulants has been improved by a greater specialization of chemoreceptor cells (Boeck et al. 1966, Rees, 1969, Schoonhoven, 1972).

It is much more difficult to understand the evolution of chemical defense. The best known chemically and most extensively studied insect allomones are defense compounds, but we know very little about the precise effect of these substances on the most significant target predators, which in fact are often not known with certainty.

However it is a well established fact that the reaction of predators to defense compounds can vary greatly (Rothschild and Kellet, 1972), and any broad generalization of quantitative results obtained with one or a few predators is hazardous. This is particularly true if the potential predators include both vertebrates and invertebrates.

Aposematic caterpillars of *Tyria jacobaeae* are greedily eaten by the carabid, *Abax ater*, which rejects with great disgust unidentified green sawfly larvae (Josens, personal communication).

It is highly probable that efficiency cannot simply be measured by the toxicity of the compound. Some optimal toxicity which is not necessarily lethal for potential predators is to be expected. This is not just because of the cost of self-protection, but also because it could be much more advantageous simply to repel a predator than to kill it. A repelled predator may turn his choice towards competitors. The only individuals that should be killed are competitors. This could explain the extraordinary antibiotic properties of ecomones released by microorganisms, whose main problem is one of competition.

The limits of chemical taxonomy

One way of understanding the evolution of a mechanism is of course to compare its aspects in related species. Quite naturally pheromones and allomones have been systematically studied in several groups of related insects. Since pheromones act at the species level, these comparisons are indeed very instructive as discussed above. However comparative studies of allomones quickly lead to chemical taxonomy which is of little value in understanding their evolution, if the comparisons do not include the whole communities.

The recent comparative studies of ladybirds' defensive alkaloids will be used to illustrate this point.

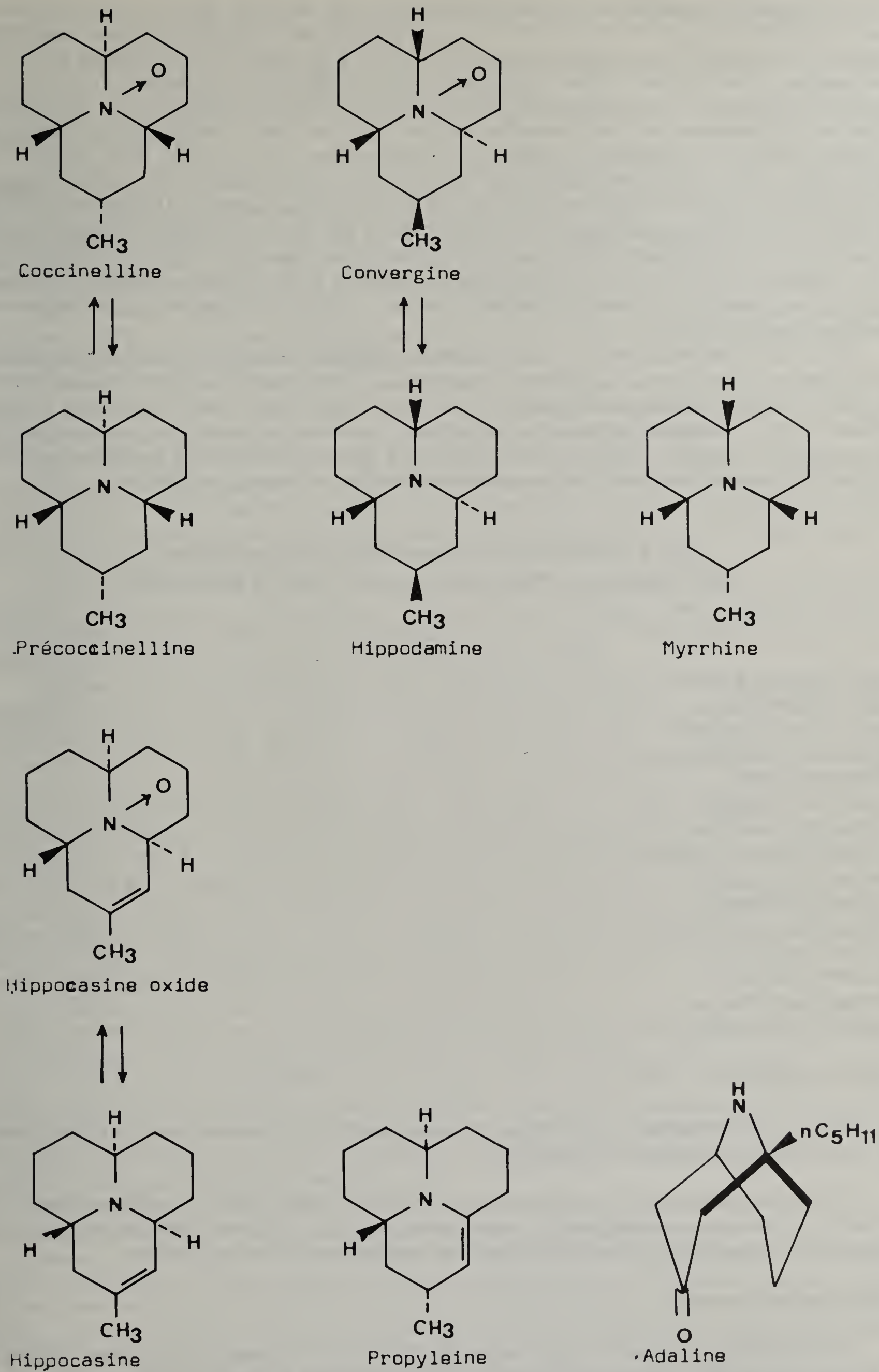


Fig. 2. —Coccinellids alkaloids (from Tursch et al. 1975, Ayer et al., in press).

Aposematic Coccinellids are well protected against ants and birds. Their strong bitter taste is due to alkaloids stored in the blood (Pasteels et al. 1973). The structures of nine alkaloids have been completely elucidated (Fig. 2) (Tursch et al. 1975, Ayer et al. in press). Their distribution within the Coccinellinae is summarised in Table 1. It is clear that this distribution is not random. For example, a remarkable constancy is observed within the same genus. While some alkaloids are very similar (myrrhine, hyppodamine and precoccinelline are the only three possible stereoisomers of the same molecule); others (like adaline) are distinctly different. Some will probably prove to be more distasteful, or toxic, than others. Preliminary tests have shown that *Adalia bipunctata* is less quickly rejected by ants (*Myrmica rubra*) and birds (quails) than *Coccinella 7-punctata* (Pasteels et al. 1973). However, it is not known whether this is due mainly to the quantity or the quality of alkaloids stored in the blood or both. Moreover the effects on a few “standard predators” could be misleading for the understanding of the evolution of such defensive mechanisms. So far *Aphidecta obliterate* is the only Coccinellinae known to be devoid of alkaloids. It has also a dull colour. This does not of course mean that this is a primitive trait.

Some of the ladybirds listed in Table 1 live in very different biotopes; *A. 19-punctata* in marshes; *M. 18-guttata*, on pine trees; *A. obliterate* on spruces; *C. 7-punctata* and *A. bipunctata* are frequent on grass and bushes, but their distribution is much wider. These beetles have thus to face a partially different array of predators and parasites, with different searching behaviors, discrimination faculties or memorization capacities. Moreover the qualities and quantities of alkaloids should be studied in relation with aposematism, colour polymorphism and possible warning odours (Rothschild, 1961).

Table 1.—Distribution of defensive alkaloids in Coccinellinae
(after Pasteels et al. 1973, Tursch et al. 1975, Ayer et al. (in press).

	1	2	3	4	5	6	7	8	9
<i>Adalia bipunctata</i> and var.	+	-	-	-	-	-	-	-	-
<i>Adalia 10-punctata</i>	+	-	-	-	-	-	-	-	-
<i>Anisosticta 19-punctata</i>	-	+	-	-	-	-	-	-	-
<i>Hippodamia convergens</i>	-	+	+	-	-	-	-	-	-
<i>Hippodamia caseyi</i>	-	+	+	+	+	-	-	-	-
<i>Coccinella 7-punctata</i>	-	-	-	-	-	+	+	-	-
<i>Coccinella 5-punctata</i>	-	-	-	-	-	+	+	-	-
<i>Coccinella transversoguttata</i>	-	-	-	-	-	+	+	-	-
<i>Coccinella 11-punctata</i>	-	-	-	-	-	-	+	-	-
<i>Coccinella californica</i>	-	-	-	-	-	-	+	-	-
<i>Cheilomenes propinqua</i> (var 4-lineata)	-	-	-	-	-	+	+	-	-
<i>Micraspis 16-punctata</i>	-	-	-	-	-	+	-	-	-
<i>Myrrha 18-guttata</i>	-	-	-	-	-	-	-	+	-
<i>Propylaea 14-punctata</i>	-	-	-	-	-	-	-	-	+
<i>Aphidecta obliterate</i>	None								

1 : adaline, 2 : hippodamine, 3 : convergine, 4 : hippocasine, 5 : hippocasine oxyde, 6 : precoccinelline, 7 : coccinelline, 8 : myrrhine, 9 : propyleine.

Chemical taxonomy is a necessary step in chemical ecology, but the understanding of the evolution of allomonal control needs a more holistic approach. We have learned a lot more about Coccinellid chemistry, but still very little about their ecology and defensive strategies.

The ecological approach

The evolution of allomonal control cannot be understood if the community is not considered as a whole. Paradoxically this ecological approach is still infrequent in chemical ecology, and is almost restricted to the study of insect-plant communities.

The role of plant allomones in the coevolution of plants and butterflies, developed by Erlich and Raven (1964) does not need to be repeated here.

It is to some extent possible to speculate about how allomonal control might evolve in complex communities, despite our poor knowledge of their functioning.

Increase in complexity, diversity and specialization. — Biological evolution is towards increasing complexity and diversity.

Communities seem to evolve towards complexity in stable environments. In such communities, it may be predicted that ecomones will increase in diversity and lead to an increasingly close interaction between their members. Indeed the “arms race” can lead to an increasing diversity of defense compounds (Janzen, 1973), and coevolution between insect and host plant often leads to specialization. Moreover, Feeny (1973) has recently aptly commented on the high probability that an insect specialist will remain a specialist and has little chance of returning to a polyphagous diet.

This evolution towards complexity and specialization might have some limits, and such ecosystems will become dynamically fragile according to May (1974). Evolution of ecomonal control in less stable environments might be completely different.

It is not my purpose to discuss at length the much debated question of ecosystem diversity and stability; my point is that a holistic approach in chemical ecology will stimulate research in this field, and at the same time could bring answers to what are still controversial questions.

From allelopathic regulation towards mutualistic communication. — Allee et al. (1949) have developed at some length the idea that the interaction between species within a community should evolve from exploitation towards mutualism. More recently Southwood (1972) has argued that such evolution is frequent in the insect plant relationship in which “the full spectrum from plant predator via parasite to symbiont can be observed.”

The strongest advocate of such evolution was certainly Emerson (in Allee et al. 1949) who considered communities as “supraorganisms.” Even if such evolution should appear as only one possibility among others, there is no doubt that it has occurred. This implies that allelopathic regulation has sometimes evolved towards mutualistic communication.

Emerson was obviously influenced by the extraordinary coevolution of the termites and their staphylinid guests. Indeed a progressive shift from simple chemical defense towards more sophisticated communication systems can readily be inferred from a study of the chemical interactions between termites or ants and their guests. Free living Aleocharines possess a large, effective, tergal defense gland. This gland is completely, or almost completely, reduced in the most advanced termitophile species (symphiles like Corotocini), but is more developed in the less specialized synoechetes. At the same time, new glandular structures have evolved in the Corotocini, the secretion of which is actively licked by the termite hosts (Pasteels, 1968a, b, 1969). The same evolution arose in the highly specialized ecitophiles (unpublished). *Atemeles* and *Lomechusa* seem to be more recent myrmecophiles, judging by their degree of similarity with free-living relatives. The defense gland is present in both species, alongside appeasement glands (at least in *Atemeles*, Hölldobler 1970). The defensive secretion of *Lomechusa* is quite similar to that of the free-living species, *Drusilla canaliculate* (Blum et al. 1971, Brand et al. 1973).

Of course social symbiosis appears as a very particular case, as an exceptional example of an extreme evolution towards interspecific integration. Other interspecies relationships may however be more mutualistic than previously thought and some so-called kairomones, less inadaptative for the sender. A signal which induces grazing seems obviously quite inadaptative for the plant. Actually grazing will sometimes accelerate primary production, as recently demonstrated by Mattson and Addy (1975) in forest primary production. In fact the relationship could shift from mutualistic in favorable surroundings for the plants to predatory in less favorable ones. This demonstrates that the concept of kairomone must be used with great care.

The comparison of communities. — A few ecologists have demonstrated that strong predictions about ecomonal control can be made when different types of communities are compared.

Janzen (1973) deduced from his detailed studies of bruchid-seed relationships in a tropical forest in Costa Rica, that there should be a character displacement in seed defensive chemistry. Seed defense compounds should be more varied within a community than between similar communities. This is a very interesting prediction, which could be extended to other predator-prey relationships, and which could be easily checked.

Feeny (1973) has speculated that biochemical “coevolution between plant and insects may differ substantially from one kind of plant community to another.” Plants less abundant and

ephemeral, would develop a "qualitative" chemical defense, i.e. the synthesis of unusual compounds in large enough quantities to repel non-adapted insects which happen to meet the plant, but not specialists against which escape is the best strategy. Plants which are bound to be found, like trees, will develop "quantitative" chemical defense, that is large amounts of unspecific toxins like tannins, which together with low nutritional value and hard exture would greatly increase the metabolic cost imposed on phytophagous insects. The first strategy would be used by herbs in temperate zones early successional communities, the second, in temperate climax forests.

Rather similar predictions have been made and checked by Oriens and coworkers (Oriens et al. 1974): the main defensive strategy of early successional annuals is escape, that of late successional and climax plants is chemical; while acute toxins would be effective primarily against generalized herbivores and concentrated in the ephemeral tissues, digestivity-reducing substances are to be expected in perennial plants or long lasting tissues such as mature leaves and woody material as a defense against specialists.

These examples, restricted to herbivore (mainly insect)-plant relationships amply demonstrate how stimulating this approach can be which indeed gives to chemical ecology its true ecological dimension.

Conclusion

My conclusion is a call for a more ecological involvement in chemical ecology.

Pheromones and allomones are holistic concepts which have had and will continue to have enormous stimulating effects on research in natural product chemistry, insect behavior and physiology.

Most studies dealing with insect allomones and pheromones start very naturally with one species, and the process is repeated over and over again, passing from species to species, leading to very instructive comparisons. The species is of course the right level at which to study the intraspecific messengers: pheromones. This is partly why, in general, our understanding of pheromone regulation seems to be so far in advance of our understanding of allomone regulation, and especially of chemical defense strategies at a high trophic level. The units in which allomones operate are of course communities. Comparative studies between species must therefore be extended to include comparisons between communities.

The study of pheromones and allomones is a multidisciplinary field that can be explored only by a close collaboration between chemists, ethologists and physiologists; the team should include more ecologists. It is very significant that the importance of pheromones and allomones in insect biology has been chosen as the general theme for the symposium of the section on insect behavior and not that on ecology.

Eisner (1972) has said that "chemical ecology is a field in which exploration and discovery are still very much in order, for the very fundamentals are still vague." This means that, however fascinating research on allomones and pheromones may already be, the best is still to come.

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The Adaptiveness of Pheromone Communication

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ABSTRACT

Chemical communication appears to be the primary channel for the exchange of information among insects. A chemical message transmitted between individuals of the same species is called a pheromone, whereas a message transmitted from one species to another is called an allomone or a kairomone, depending on whether the transmitter or the recipient, respectively, of the message benefits from the communication sequence. The chemical messages are often composed of mixtures of compounds, with the precise behavioral role of the individual compounds being poorly understood. In many cases, the same secretion functions simultaneously as a pheromone and an allomone and/or a kairomone. For example, the "pheromone" released from a female moth that is ready for mating may cause approach and copulatory behavior of conspecific males (pheromone function) and, at the same time, deter these behaviors in males of related species (allomone/kairomone function). Similarly, ants during times of danger may release secretions that cause species mates to disperse (pheromone function), while immobilizing the potential enemy (allomone function). The communication sequences have become finely adjusted through evolutionary selective pressures so that they are appropriate to the way of life of the particular species involved, the environmental context within which the communication process occurs, and the physiological status of the communicating individuals.

Although many insects have the ability to communicate using the same five sensory modalities that are used by man — vision, hearing, touch, taste, and smell — plus probably some modalities not yet recognized by man, their sensing of the environment, including their sensing of others of the same species, appears to be accomplished mainly by the chemical senses of smell and taste. Those chemicals that are used for communication between individuals of a given species are called pheromones. More specifically, a pheromone is defined as a chemical or a mixture of chemicals that is released to the exterior by an organism and that causes one or more specific reactions in a receiving organism of the same species (Karlson and Butenandt 1959, Karlson and Luscher 1959). Note that the mode of production of the pheromone is not a consideration in this definition (Shorey 1976). The chemical or chemicals may be taken in from the environment by the organism and then released intact as the pheromone, or the pheromone chemicals may be synthesized *de novo* by the releasing individual or by symbionts within the releasing individual. In fact, in most cases, the manner of biosynthesis of pheromones has not been elucidated.

Unfortunately, the definition of a pheromone as one or more chemicals which operate to release one or more specific reactions still lacks rigidity. Such a definition was more acceptable a decade ago when, with the exception of investigators of ant alarm pheromones, most investigators felt that insect pheromones typically consisted of single chemicals. We now know that blends of chemicals are the rule rather than the exception for most classes of pheromones that have been studied intensively, and that the types and amounts of the various components of a pheromone mixture often determine its biological activity. As will be discussed below, the more-than-30 chemicals in the Dufour's gland of an ant might be regarded in combination as being an alarm

pheromone. However, "alarm" is not a simple reaction; it is a complex behavior that often is composed of sequential steps, with one step perhaps being released by one specific combination of the chemicals and the next being released by another specific combination. With rigorous adherence to the definition, then, we would say that there is a different pheromone from the pheromone glands of a given ant species for each specific step in a behavioral sequence that requires a different chemical blend for its release.

In the same vein, scolytid beetle aggregation, as will be discussed below, is often stimulated by a specific blend of chemicals, some of which are produced by the beetles themselves and some by the host trees. The beetle-released secretions may be inactive in causing certain behaviors without the simultaneous presence of the host tree chemicals. Are secretions which are inactive alone to be called pheromones? To avoid being embroiled in semantic considerations, for the remainder of this paper broad generic categories of pheromones will be specified: the so-called alarm pheromones of ants, aggregation pheromones of scolytid beetles, and sex pheromones of moths. Such a terminology sidesteps the semantic problems by referring to the end result of the various behavioral reactions — alarm, aggregation, and sex — instead of to the detailed behavioral reactions themselves.

Pheromone communication, although seeming at first glance to entail a simple release of a chemical stimulus by one individual and an automatic response to the stimulus by a receiving individual, is found after detailed study to be much more complex than this. The manner of production and release of the message and the manner of response to the message have evolved in a way that maximizes the likelihood that successful communication will occur at the right time and under the right circumstances to ensure the well-being, survival, and maximum reproduction of the communicating individuals. Thus, no two pheromone-communication systems, displayed by different species, are truly identical. Instead, each communication system has been molded by natural selection to the extent that it is appropriate to the way-of-life of the particular species and functions best when the insect is in the correct physiological state and senses the correct environmental context under which the communication process normally occurs. This appropriateness, this fitting correctly with the environmental context, is rarely seen in the artificial laboratory situations under which most pheromone studies are conducted. Expecting normal behavior from an insect exposed to a pheromone in the laboratory, without due consideration for all the environmental and physiological variables that must be appropriate in order for that behavior to be displayed normally, may be analogous to enclosing a human in a cage (with a lion) and then asking him which of two perfume odors is the most stimulating. The situation must be appropriate for communication before communication will occur normally, and a variety of adaptations have evolved to assure that this occurs. Some of these adaptations are nicely illustrated by our present knowledge — admittedly still very incomplete — regarding the alarm pheromones of ants, the aggregation pheromones of scolytid beetles, and the sex pheromones of moths.

Ant Alarm Pheromones

Alarm pheromones constitute a diverse group of pheromones that have in common the fact that they are typically released when an individual perceives a threatening situation or is injured. These pheromones cause a great variety of behavioral responses depending on the species involved, the precise blend of chemicals that the responding individual perceives, the concentration of the chemicals that it perceives, the caste and physiological condition of the responder, and the environmental context in which the message is received.

Probably the most frequent threatening situation which leads to release of an alarm pheromone by ants of many species is the presence of ants of other species or even ants from other colonies of the same species. The foreign ants might be of a type that would plunder the food stores of the defended colony, would carry off its young as potential slaves, or would compete for foraging materials in the area near the defender's nest. Obviously, it is adaptive for the defenders to recognize and destroy the first invaders of their territory before the invaders can organize a raid or can initiate foraging in that area (Wilson 1975).

In some instances the alarm pheromone chemicals may not indicate a threat at all; instead, they may be released — at least in some species — when scouts detect a prey animal that is to be subdued, chopped up, and carried to the nest.

Ant alarm pheromones are produced in glands located in close proximity to the organs of aggression and defence — the mandibles and sting (Maschwitz 1966, Wilson and Regnier 1971). In

fact, many of the chemicals used as alarm pheromones or present in the same secretions with alarm pheromones produce an irritating, immobilizing, or toxic action when directed against other animals. Further, it is possible that the defensive role of the secretions arose before their role of alerting colony-mates to potential danger (Blum 1974). This dual function, with the same secretion which is directed defensively against an enemy also alerting nest mates to help subdue the enemy, represents a considerable economy of effort.

Chemicals found in ant alarm pheromones fall into a variety of chemical groups, although they are mainly short-carbon-chain terpenes, ketones, and alkanes (Wilson and Regnier 1971). The blend of chemicals produced in one gland may be very complex. As mentioned earlier, more than 30 constituents have been identified from the Dufour's gland (which together with the poison gland emits its secretion via the sting) of a number of ant species (Bergström and Löfqvist 1972). Volatilities and diffusion rates of the chemical constituents in the secretion may vary considerably. In the still air in the ant nest, the chemical message spreads mainly by diffusion and stimulates other ants within the active space (that space which contains the appropriate chemicals at above the threshold for causing a biological response) to perform appropriate behaviors. In the field away from the nest, the chemical message is carried by some combination of air flow and diffusion.

The time-course and intensity of the pheromone message may vary depending on the severity of the disturbance which led to release of the pheromone. This is illustrated nicely in research by Wilson and Bossert (1963), who found that if all the alarm pheromone contained in the mandibular glands of an ant of the species *Pogonomyrmex badius* was liberated instantly by crushing its head, the zone of the active space of the pheromone odor would attain its maximum radius of about 6 cm in 13 sec. Within 35 sec, the active space and, therefore, the behavioral effect of the chemical, would fade out completely due to diffusion. If the worker were merely threatened and not crushed, it might release some smaller quantity of the pheromone, proportional to the degree of threat. The resulting active space would then be smaller and fade away more rapidly. Thus, with a small disturbance in the nest, the number of workers influenced by the pheromone is relatively small, the disturbance is quickly subdued, and the signal rapidly dissipates. With a larger disturbance, a correspondingly larger amount of pheromone released activates a larger group of workers (some of whom might release pheromone themselves), and the signal and resulting mobilization of forces persist longer. For any size alarm pheromone signal, its rapid fade-out prevents a lingering effect which might disrupt colony activities after the threatening situation is removed or which might affect a larger part of the colony than is necessary.

Diverse behavioral reactions are displayed in response to ant alarm pheromones, all of the reactions presumably having evolved because they maximized the likelihood of colony survival and reproduction. In the most general terms, Maschwitz (1966) proposed that if ants are foraging away from the nest vicinity and perceive their species' alarm pheromone, they typically disperse from the area. This behavior appears adaptive, maximizing the likelihood that the ants would then return safely to the nest. On the other hand, in the nest or in its immediate vicinity, the alarm pheromone often causes the ants to approach the pheromone source and display aggressive behavior; this behavior again appears adaptive, resulting in the defense of the nest with its queen, food stores, and young from enemy attack. Furthermore, Wilson and Regnier (1971) generalized that ants of species having large, compact colonies tend to respond to disturbances with approach and aggressive behavior, whereas ants of species with small or diffusely distributed colonies tend to disperse under similar circumstances.

An enemy or a prey animal may in some cases become distinctly labeled with the alarm pheromone, which the ants deposit on it by spraying or during the aggressive activities of biting or stinging. Aggressive behavior by other ants of the species then usually seems to be triggered by an interaction of the pheromone stimulus plus appropriate stimuli which come directly from the enemy. However, it has been demonstrated in certain ant species that the alarm pheromone alone can cause aggressive behavior, without additional stimuli from the enemy. Thus, ants of some species open their mandibles in an aggressive response when they perceive the correct concentration of appropriate alarm pheromone chemicals (Fales et al. 1972, Moser et al. 1968, Regnier and Wilson 1968).

In early research, it was mainly assumed that various concentrations of the total pheromone — consisting of one or more components — caused the various behavioral steps which taken together are regarded as alarm behavior. For example, under the correct circumstances, low concentrations might lead to alerting and activating of the ants, intermediate concentrations might cause their attraction toward the chemical source, and still higher concentrations might evoke attack behavior. Much of this

concept probably needs to be modified in the light of recent research which shows that the secretions from certain glands may cause some of the behavioral reactions and those from other glands may cause other reactions, and even that certain components of the pheromone blends may cause some of the behavioral reactions, while other components may cause other reactions (Bergstrom and Löfqvist 1970, Blum 1974, Bradshaw et al. 1975, Cammaerts-Tricot 1975, Löfqvist 1976, Robertson 1971).

An example of such complexities, with different behavioral reactions being stimulated by the various pheromone components, and also a demonstration of different behaviors being displayed by different castes, is seen in the ant, *Oecophylla longinoda* (Bradshaw et al. 1975). Colony defense is carried out almost exclusively by the major workers, which function as soldiers. The minor caste remains in the nest until it is directly disturbed. Both castes produce multichemical alarm pheromone secretions in their mandibular glands, poison glands, and Dufour's glands. Some of the alarm pheromone components released from the mandibular glands of minor workers serve to disperse others of this caste, while at the same time attracting major workers. This difference would appear to maximize survival of the colony and lead to rapid elimination of enemies. The major workers exhibit at least 4 different steps of behavior in response to the mandibular gland secretion released from their own caste. These are (1) alerting, with the ants raising their heads and opening their jaws, (2) attraction toward the chemical source, (3) arrestment of locomotion near the chemical source, and (4) biting. Among the chemicals isolated from the secretion, the more volatile ones appear to cause the early steps in the sequence and the less volatile the later steps. It would appear that a sequential message of pheromone signals occurs when the total alarm pheromone blend is released, with concentric active spaces of the individual components being formed. The extent of the active space for any one component depends on the volatility of that component and the threshold for response of ants that are exposed to it. With the active spaces of those components that cause alerting and attraction being relatively large and of those causing arrestment of locomotion and biting relatively small, behaviors are stimulated in the proper sequence to result in effective attack against an enemy. A similar, somewhat-more-complex behavioral scheme has been described for the ant *Formica rufa* by Löfqvist (1976). Future study will undoubtedly reveal even more complexities, with the various alarm pheromone components from the various glands of the various castes leading to appropriate behaviors by members of each caste at appropriate times.

An important component of alarm behavior in some species is the inhibition of aggression against fellow nest-mates, which otherwise might be indiscriminately attacked in the melee that takes place under the influence of a high alarm pheromone concentration. Apparently, certain chemical constituents of the ants' glandular secretions remain associated with the releasing ants and serve to inhibit the aggression of nest mates toward them (Tricot et al. 1972).

Still another variant of alarm behavior has been observed in the myrmicine ants *Pheidole dentata* (Wilson 1975) and *Myrmica rubra* (Cammaerts-Tricot 1975). In both species, some of the workers, when stimulated by the alarm pheromone, return to the nest depositing a pheromone trail on the ground, from the poison gland via the sting, as they proceed. In the case of *M. rubra*, the trail-forming workers then proceed back to the alarm source, following the same trail, and depositing an additional pheromone from their Dufour's gland. Then, that caste that serves as soldiers (in *P. dentata*) or the oldest workers (in *M. rubra*) follow the trail from the nest to the enemy and, partly in response to additional pheromone components that have been released by their nest mates near the enemy, attack and subdue it. During this time, the minor caste (*P. dentata*) or the younger workers (*M. rubra*) do not tend to engage in the direct conflict, although they do lay the trails that recruit ants of the aggressive castes.

Many of the alarm pheromone components are widely distributed, being found in a number of species, and in some cases some of the components of the pheromone blend released from one species could incite aggressive responses by members of another species. However, because the range of ant alarm pheromone communication is usually limited to a few cm, and because alarm pheromone release usually occurs in the territory lying close to or in the nest of a given colony, only the insects belonging to that colony will be available to respond, making any lack of species specificity of little importance in nature. An exception to this generality is found in certain slave-making ants which release massive quantities of alarm pheromone when raiding the colonies of other species. The pheromone effectively disrupts the behavioral activities of the raided colony while at the same time recruiting more individuals of the raiding colony (Regnier and Wilson 1971).

Bark beetles and ambrosia beetles utilize efficient chemical communication systems that result in large populations concentrating in suitable host trees. Depending on the species of beetle, the trees which they colonize may be healthy, weakened, dying, or dead. Successfully invading beetles bore through the bark and construct tunnels in which they mate and lay their eggs. The ensuing larvae tunnel further through the xylem, phloem, or bark. The colonization process is often highly efficient, with almost all available space and resources being used by the large numbers of beetles that aggregate in a given tree.

For most species that have been studied, a complex of pheromonal stimuli released by the invading beetles, in combination with a variety of stimuli that emanate from the host trees, regulate beetle behavioral reactions to ensure that optimal colonization by individuals of both sexes occurs. Chemical stimuli from the beetles and the trees also often operate to terminate the colonization process before overcrowding takes place.

The beetle reactions are modulated by a large number of physiological and environmental variables, such as daily rhythms, temperature, humidity, light intensity, and the previous occurrence of appropriate behavioral activities. These variables are not discussed here, because the influence of such factors is explored in some detail in the next section, in relation to moth sex pheromones.

Colonization starts with alightment on a suitable host by an initially invading beetle. As a rule, in monogamous species (such as *Dendroctonus* species), the females are the initial invaders, while for polygamous species (such as *Ips*), the males typically initiate the attack (Borden 1974). Volatile chemical stimuli from the tree, often operating in conjunction with visual stimuli associated with the image of the tree, guide the approach of the initial invaders (at least for some species that have been studied).

In many species that attack weakened trees, the initial invaders bore their entry tunnels through the bark and then release pheromone with their feces (Pitman and Vité 1963, Pitman et al. 1965, Vité and Pitman 1967, 1968, Wood and Bushing 1963, Wood et al. 1966, Zenther-Moller and Rudinsky 1967). If the tree is too healthy and therefore inappropriate as a host, the invader is killed by the copious flow of resin at the site of attack before releasing its pheromone message. In the species that attack healthy trees, pheromone may be released by the initial invaders before they tunnel into the bark; this early release of the aggregation stimulus appears highly adaptive, considering the probability that the first invaders will be killed and that many other invaders must be recruited to initiate tunnels until the tree becomes sufficiently weakened as a result of the mass attack that its resin flow diminishes and successful beetle establishment can occur (Borden 1974, Vité et al. 1964, 1968, Vité and Renwick 1968, Vité et al. 1972).

The pheromone chemicals secreted by the initial invaders, often operating in conjunction with volatile chemicals released from the attacked host tree, cause the recruitment of beetles of both sexes to the host. The host odorous compounds have generally been found to be terpene resins, although recent research has indicated that non-terpene volatile compounds may be involved also (Billings et al. 1976).

The behavior of the recruited beetles varies according to sex. Those of the same sex as the initial invaders bore new entry tunnels and release pheromone, thereby increasing the concentration of these odorous compounds in the nearby air and stimulating even more beetles to approach the tree. Beetles of the opposite sex, which also may release a pheromone when they arrive at the tree, are stimulated to enter the tunnels made by the initially invading sex, wherein mating occurs and eggs are laid. In a number of experimental studies, investigators have found that certain scolytid species, upon encountering high concentrations of the aggregation-inducing chemicals, tend to visually orient to vertical (or in some cases horizontal) objects. The behavior seems to be adaptive, since such objects in the beetles' natural environment are likely to be the trunks of the trees or the logs from which the pheromones are volatilizing (Gara and Coster 1968, Gara et al. 1965, Vité and Pitman 1969, Vité et al. 1964).

A number of complex behavioral responses must occur among beetles of both sexes to ensure that the host is optimally colonized. During the course of colonization, the changing concentrations of pheromone and of host-tree volatile chemicals, plus the different blends of constituents in the pheromones secreted by male and female beetles, often determine the number and the sex ratio of the additional beetles that are recruited (Bedard et al. 1969, Borden 1967, Furniss and Schmitz 1971, Gara et al. 1965, Gray et al. 1972, Jantz and Rudinsky 1965, Peacock et al. 1971, Peacock et al.

1973, Pitman 1969, Pitman and Vité 1969, Rudinsky 1973, Vité and Pitman 1968, Vité et al. 1964, Wood 1970, 1972).

The scolytid beetle aggregation pheromones are typically complex, often consisting of 3, 4, or more chemical components manufactured by each sex. However, in most cases, the exact behavioral roles of the individual chemical components that make up each pheromone blend are unknown.

When a beetle is flying toward a tree under the influence of the aggregation-inducing stimuli, appropriate stimuli must then be encountered to cause it to cease flight and alight. In some species, the cessation of flight activity is apparently caused by the high concentrations found near the tree of the same pheromone chemicals that induced the approach flight from a distance. However, it is likely that the blend of chemicals which is responsible for inducing the approach flight may often be different from the blend that finally arrests flight activity (Bennett and Borden 1971, Borden 1974, Rudinsky 1973, 1974).

Interchanges of a variety of stimuli ensure that the two sexes get together in the tunnels. A beetle may be arrested in its locomotion when it perceives the high pheromone concentration near the entrance of a tunnel made by the opposite, initially invading sex. It then may be stimulated to emit characteristic communication sounds (at least in many species) and to enter the tunnel, after perceiving some combination of the volatile pheromone stimulus, a gustatory stimulus from the pheromone-permeated frass near the tunnel entrance, and sonic and other stimuli from the occupier of the tunnel (Bennett and Borden 1971, Jantz and Rudinsky 1965, Wood and Bushing 1963, Wood et al. 1966). At this time of stimulus interchange between the tunnel occupier and a beetle of the opposite sex which is about to enter the tunnel, one or the other of them (depending on the species) may release another pheromone into the air which is antiaggregative, causing other flying beetles to not approach or alight in that immediate area (Furniss et al. 1972, Kinzer et al. 1971, Libbey et al. 1974, Michael and Rudinsky 1972, Rudinsky 1969, 1973, Rudinsky and Michael 1972, 1974, Rudinsky et al. 1972, 1973, 1974).

A number of factors, which differ from one species to another, prevent additional beetles from aggregating after the tree has become optimally colonized (Gara and Coster 1968, Gara et al. 1965, Nijholt 1970, 1973, Rudinsky 1969, 1973, Rudinsky et al. 1974, Vité and Pitman 1969). These factors include (1) a build-up in the air of the aggregation-inducing pheromone concentration to such a high level, due to the arrival of and pheromone-release by large numbers of recruited beetles, that additional approaching beetles are stimulated to arrest their flight and to visually orient to nearby trees when they are still downwind from the actual target tree, (2) the release by beetles of either the initially invading sex or their potential mates of anti-aggregative pheromones at such a high concentration that the approach of additional beetles to the entire tree becomes inhibited, (3) cessation of release of volatiles from the host tree as it becomes weakened through beetle attack, and/or (4) cessation of release of aggregation pheromone by beetles in the various tunnels after their mate-attracting activities have been completed.

Those chemical components of scolytid aggregation pheromones that have been identified are mainly terpenoids, and they bear a marked resemblance to many of the chemicals that occur in the host-tree resin. In fact, recent experiments have indicated that the host terpenes may be metabolized within the insects, in some cases by intestinal symbionts, resulting in the formation of certain of the pheromone components (Brand et al. 1976, Hughes 1973, 1974, 1975, Renwick et al. 1973, 1976).

Lepidoptera Sex Pheromones

This section is restricted to a consideration of the sex pheromones that are released by female moths prior to mating and that stimulate males to perform a variety of behavioral reactions that terminate in their copulation with the females. Major emphasis is devoted to a discussion of how pheromone production and release by the females and pheromone responsiveness by the males are controlled and modulated by physiological characteristics of the insects and by various environmental parameters so as to maximize the likelihood that communication between the sexes will occur under the most appropriate circumstances for successful mating.

The detailed behavioral reactions that are exhibited when male moths are exposed to a female sex pheromone vary from species to species. The following general scheme which has been determined for *Trichoplusia ni* is probably representative of that followed in many moth species. The reactions occur in a sequence or hierarchy, with the successive steps often being stimulated through the male's perceiving the successively higher pheromone concentrations as it approaches the female

(Shorey 1976). However, in some species the successive steps might be caused because a male moth perceives the critical concentration of certain pheromone components that stimulate behaviors occurring early in the response sequence when he is at a great distance from the emitting female and the critical concentration of other components that stimulate later-occurring behaviors when closer to the female (Cardé et al. 1975b, c).

A resting male of *T. ni*, upon stimulation by sex pheromone which is being continuously emitted by a female located some distance upwind, exhibits the following responses in sequence (Gothilf and Shorey 1975, Ignoffo et al. 1963, Shorey 1964, Shorey and Gaston 1970).

- (1) He brings forward his two antennae, which were previously positioned under the leading margin of his wings.
- (2) He spreads his wings and vibrates them with increasing amplitude, apparently resulting in the warming of the flight muscles.
- (3) He takes flight.
- (4) He follows the aerial pheromone trail toward the pheromone source, using a variety of little-understood behavioral reactions, including anemotaxis and chemotaxis.
- (5) He reduces his forward flight speed as he approaches the pheromone source.
- (6) He becomes increasingly sensitized to approach visual objects, which may in nature represent substrates to which pheromone-releasing females might be clinging.
- (7) He also becomes increasingly sensitized to approach visual objects of the approximate size of a female moth.
- (8) He hovers in flight behind and below the female's abdomen tip.
- (9) He often touches the vicinity of the female's pheromone gland with his antennae and fore tarsi.
- (10) He curves his abdomen toward the female and everts his hair pencils (possible pheromone disseminators), apparently directing the hair pencils toward the female's head.
- (11) He curves his abdomen tip toward the female's abdomen tip in a copulatory attempt.

This entire sequence also occurs if a small spot of female sex pheromone is placed on filter paper, although the accurate orientation of the reactions in steps 8-11 requires the presence of a model approximating a female moth.

The production and release of the pheromone by female moths and the responses of pheromone-stimulated males are influenced by a variety of physiological parameters, including age, circadian rhythms, mating history, and habituation and sensory adaptation (in males) following prior exposure to the odor. Environmental variables that affect pheromone behavior include light intensity, temperature, air velocity, and the nature of the surrounding vegetation.

Age is an obvious factor, although the emphasis should be on reproductive age rather than temporal age. It would not be adaptive for a female to release pheromone if her reproductive system were not yet prepared for proper utilization of sperm in inseminating the eggs or for properly storing the sperm. Similarly, it would not be adaptive for a male to be responsive to pheromone if his ability to transfer sperm has not matured. Thus, in the few studies that have been conducted on this matter, it has been found that female pheromone production and release occurs near the time when the eggs are being matured in the oviducts and males do not respond until they are capable of mating (Payne et al. 1970, Shorey et al. 1968a, b, Steinbrecht 1964). The antennae of males of *T. ni* are capable of responding to female sex pheromone even before the males emerge from the pupal case, although the males do not respond behaviorally until one or two days following emergence, indicating that the control center for the age of pheromone responsiveness must be located within the central nervous system (Payne et al. 1970).

Mating behavior of moths is often restricted to certain characteristic times during each 24-hour day, with the exact time periods differing from species to species. As would be expected, the release of pheromone by females and the maximum responsiveness to the pheromone by males typically occur during the mating-time period. The timing of these communication behaviors is often controlled by circadian rhythms which are entrained through a previous sensing of day-night cycles by the moths (Cardé and Roelofs 1973, Cardé et al. 1975a, Fatzinger 1973, Grant et al. 1975, Ohbayashi et al. 1973, Sanders 1969, Sanders and Lucuik 1972, Schröter and Lange 1975, Shorey and Gaston 1965a, Sower et al. 1970, 1971, Traynier 1970a). Often, the period during which males are responsive is longer than and overlaps the period when females are likely to release pheromone, thus maximizing the likelihood that a releasing female can attract a male for mating. The prevailing temperature may regulate the exact time in each 24-hour cycle when the pheromone behaviors are

expressed. For example, in some nocturnal species, the time of pheromone communication (pheromone release by females and maximal responsiveness by males) occurs during the middle or latter part of the dark period when the prevailing temperature is relatively warm. However, cooler conditioning temperatures lead to a shift in the time of expression of this rhythmic behavior, with it now being exhibited earlier in the dark period (Cardé and Roelofs 1973, Cardé et al. 1975a, Saario et al. 1970, Sower et al. 1970, 1971, Truman 1973). This change in timing according to the ambient temperature would appear adaptive, causing the insects to communicate earlier on cool nights, before the temperature drops so low as to inhibit behavioral activity. Conversely, females of a day-active moth, *Synanthedon pictipes*, release pheromone later during the light period when temperatures are low than when they are high, again apparently maximizing the likelihood that mating behavior will occur under the most favorable, warm-temperature conditions (Gorsuch et al. 1975).

Some of the selective pressure which resulted in distinct circadian rhythms of moth sex pheromone behavior might be attributed to the advantage associated with mating at a time different from the mating time of closely related species, which might otherwise be cross-attractive in their pheromone communication systems. Thus, when two closely related species are located in the same geographic area during the same time of year, they are often found to have distinctly different time periods when they communicate (Shorey 1974).

The influence of mating history on female pheromone production varies with the species. Females of those species that mate only once during their lives do not tend to release pheromone again after the mating, and the amount of pheromone contained in their glands often decreases rapidly after mating has been accomplished (Collins and Potts 1932, Perez and Lang 1964, Steinbrecht 1964). For females of other species that mate more than once, pheromone must be released again because this is the phenomenon that initiates the communication process between the sexes; in these species, the pheromone content in the gland remains high, although it may be reduced somewhat when compared to that of virgin females (Adeesan et al. 1969, Brady and Smithwick 1968, Fluri et al. 1974, Minks and Noordink 1971, Richerson et al. 1976, Shorey and Gaston 1965b, Shorey et al. 1968a). Mated females of *T. ni*, although still tending to release pheromone and thus mate again on some night after an initial mating, release pheromone for much briefer time intervals than do virgins (Bollinger and Shorey, unpublished data), thus increasing the probability that most of the virgins in a population will be inseminated before much multiple mating occurs. I suspect that males of most moth species also have a refractory period, ranging from a few hours to a day following mating, during which time their reproductive systems are being primed again for sperm transfer and during which time they are totally unresponsive to pheromone. However, since the males of most moth species are multiple maters, they must become responsive to the female sex pheromone again at some time after any one copulation (Shorey and Gaston 1964).

A male moth, after exposure to the female sex pheromone odor, exhibits for some time a reduced responsiveness to the odor even if the first exposure did not result in successful copulation (Bartell and Lawrence 1973, Bartell and Roelofs 1973, Bartell and Shorey 1969, Boeckh et al. 1965, Ignoffo et al. 1963, Payne et al. 1970, Schneider 1969, Shorey and Gaston 1964, Traynier 1970b). The reduction in responsiveness is caused by a combination of sensory adaptation at the olfactory receptor level, which typically persists for a period of seconds or minutes following the exposure, and habituation, which is not well defined but probably often represents an inhibition of responsiveness in the central nervous system and persists for many minutes or even hours. The reduction in male responsiveness appears to be advantageous in at least two ways. First, a male ceases to be responsive and therefore does not, for an indefinitely long period of time, direct sexually oriented behavior toward a pheromone source which is not an appropriate mating partner, as, for example, a female that has just received another male in copulation but is still emanating pheromone. Secondly, and perhaps even more important, sensory adaptation and habituation may adjust the responsiveness of males to a level that is appropriate to the circumstances. Consider an area containing a high population of moths of a given species, with many females already having released pheromone and attracted males to them for copulation. It would seem biologically appropriate for the remaining male moths to equate the prevailing level of pheromone in the air to "0" concentration — that is, to be unconscious of the prevailing level — until a new, nearby female starts to release pheromone. Then the males would still be responsive to that new level of pheromone which is greater than the ambient concentration in their environment. Under such conditions, the male responsiveness level and, therefore, the potential communication distance would be reduced, but even this reduction would

appear to be adaptive under such high density conditions, when the most efficient communication distance might be about 1 meter rather than 10 meters or more.

Light intensity, in addition to having an indirect, though major role in controlling pheromone communication behavior through the entraining of circadian rhythms in response to a sensing of day:night cycles, often plays a direct role by inhibiting female pheromone release or male pheromone responsiveness when the intensity is at an inappropriate level. In general, for the few species that have been studied, the direct effect of light intensity on sex pheromone communication is related to the time of day when communication typically occurs. Thus, in *T. ni*, which typically mates at night, light intensities greater than 0.3 lux — equivalent to full moonlight — inhibit the tendency of females to release pheromone and of males to respond to the pheromone (Shorey and Gaston 1964, Sower et al. 1970). Another species, *Epiphyas postvittana*, typically mates at dusk, and only those light intensities higher than 3.5 lux inhibit male responsiveness (Bartell and Shorey 1969). Finally, adults of *Carpocapsa pomonella* often mate before sunset, and males respond to pheromone-releasing females used as bait in traps even when light intensities are as high as 50,000 lux (Batiste et al. 1973). In addition to these permissive or inhibitory effects, light intensity may have a more stimulatory effect on pheromone communication behavior; for instance, Cardé and Roelofs (1973) and Cardé et al. (1975a) have shown that the decreasing light intensity that occurs at dusk directly stimulates females of the moth species *Holomelina immaculata* and *Argyrotaenia velutinana* to start releasing pheromone.

The temperature ranges that are most suitable for sex pheromone communication appear to be adaptively related to the way-of-life of the particular species, with day-active forms having a higher temperature range favoring sex-pheromone communication than do night-active species. Thus, day-active species such as *Lymantria dispar* and *Synanthedon pictipes* tend to communicate only at temperatures above 20°C (Collins and Potts 1932, Gorsuch et al. 1975), while the night-active species *T. ni* communicates by pheromones at temperatures as low as 12° (Shorey 1966, Sower et al. 1971). In addition, decreasing temperatures interact with decreasing light intensities at dusk to stimulate the females of *A. velutinana* and *H. immaculata* to release pheromone and, apparently, the males of these species to be responsive to the pheromone (Cardé and Roelofs 1973, Cardé et al. 1975a), thus assuring a synchronization of pheromone-communication activities of the two sexes at the appropriate time. An additional influence of the prevailing temperature in determining the general time during the day or night that circadian-rhythm-controlled sex-pheromone-communication activities are expressed was mentioned earlier.

Air velocity is an important factor in determining whether effective pheromone communication occurs, the distance over which it occurs, and the location in the environment at which it occurs. The velocity range which allows communication to occur may be very narrow. Too low a velocity, perhaps lower than a few tenths meter per sec. may not allow a sufficiently cohesive aerial trail of the odor to extend downwind from the releasing female and may necessitate a long time of pheromone release before the odorant trail extends any considerable distance downwind. Too high an air velocity, above several meters per sec., exceeds the flight speed of many male moths and therefore obviously prevents them from approaching their target. Within this narrow range the lower velocities theoretically enable the longest aerial trails to be formed, largely because more pheromone is emitted into each unit volume of air flowing past the female (Wilson and Bossert 1963). Although the phenomenon has not been well studied, a number of adaptations enhance the ability of moths to sense air velocity and adjust their activities in a way that maximizes the likelihood of successful communication. Thus, both males and females of *Pectinophora gossypiella* appear to sense air velocity and, when it is too high near the top of the cotton foliage where they normally aggregate prior to pheromone communication, they move to a lower level in the foliage canopy, to a position where the velocity may be at a more favorable level (Kaae and Shorey 1973). Females of *T. ni* also react to various air velocities by seemingly adaptive behaviors. When the velocity is relatively high, they tend not to vibrate their wings while releasing pheromone, whereas at lower velocities their tendency to vibrate their wings increases (Kaae and Shorey 1972). The wing-vibration behavior creates a local air current behind each female, increasing the rate of pheromone evaporation from her pheromone gland and also tending to distribute the pheromone in a more discrete aerial trail behind her; these factors might aid male close-range orientation to the female. Additional, females of *T. ni* are more prone to release pheromone when the air velocity is 0.3 to 1.0 meter per sec — perhaps the most suitable range for communication — than at higher or lower velocities (Kaae and Shorey 1972).

The surrounding vegetation also may exert an important influence on pheromone communication. Thus, pheromone communication of a number of relatively monophagous species appears to be restricted to an environment containing the appropriate plants on which their larvae can feed. The effect may be exerted on the females, which do not release pheromone unless they sense the correct plant environment (Riddiford 1967, Riddiford and Williams 1967a, b) or upon males, which might not respond to the pheromone odor unless in the correct environment (Brader-Breukel 1969). Or, the males and females might only occur in that location anyways, being already there through maturing in that environment or through being attracted into that environment prior to pheromone communication. At any rate, this environmental relationship is obviously adaptive, causing the females to be in the right location for depositing their eggs following mating. Also, the vertical location of males and females prior to communication appears to often be influenced by the local vegetation. At least for many species, the moths appear to usually communicate for mating near the top of the foliage canopy (AliNiazee and Stafford 1972, Kaae and Shorey 1973, Miller and McDougall 1973, Saario et al. 1970, Sharma et al. 1971); this observation is based mainly on studies of the optimal height at which males are attracted to pheromone-baited traps, and it is only inferred that females might also most likely be found at the same elevations. These host relationships may make the communication process more efficient by causing males and females to be concentrated in the same relatively small portion of the environment before pheromone communication occurs.

Conclusion

A major aspect that has received little attention in this paper involves the transmission of appropriate information to other species through the same chemical message that is being simultaneously used to transmit information to others of the same species. This multiple role of the chemical message is seen in relation to each of the three major types of pheromone communication discussed above. For instance, ant alarm pheromones typically also have a defensive role, being repugnant or even toxic to potential enemies. Certain components of the scolytid beetle aggregation pheromones that cause other beetles of the same species to colonize a particular tree operate to inhibit colonization by related species, thus preserving the host for the pioneer species. Similarly, certain components of some female moth sex pheromones that cause the pheromone blend to stimulate appropriate premating behaviors by males of the correct species inhibit such behaviors by males of related species.

Our knowledge of the complexities of insect pheromone behavior is still in a primitive state. The more we learn, the more we understand that the communication does not occur in a simple, automatic way, regardless of the environmental and physiological conditions affecting the insects. Instead, the communication processes are marvelously adaptive, having evolved in a manner that causes them to function best under those conditions that are most appropriate for communication.

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Aspects of Nervous Coding of Sensory Quality in the Olfactory Pathway of Insects

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ABSTRACT

At the receptor level, a few hypotheses can be set forth on the neurophysiological basis of odor discrimination. With "simple" stimuli, such as the sexual attractant pheromone of the silkworm, one single compound is effective for one type of highly specialized receptor cell. Only a certain level of excitation in this single alarm input is needed to trigger the searching behavior of the male. Other natural odors, like complex pheromones and especially food odors, consist of several or many compounds which act as odorous stimuli. Such complex odors are coded by complex patterns of activity in a whole array of different receptor types.

On the basis of neuroanatomical and neurophysiological investigations, several modes of connections are postulated between receptor inputs and central neurons in the first central olfactory relay, the deutocerebrum. Deutocerebral neurons are grouped into a few functional types with more or less specific response characteristics and filter properties for certain types of olfactory stimuli.

Introduction

Many pheromones act as olfactory signals which carry information between individuals and thereby elicit specific behavior patterns. This can be achieved only by highly selective and specific detection and discrimination mechanisms which are located in the sense organs and in the nervous system. Therefore, our understanding of pheromone effects depends highly on our understanding of the function of the receiving and integrating networks of the chemosensory pathways.

Because of their highly specific effects, pheromones belong to the favourite stimuli for sensory physiologists since there are not many stimuli that can trigger full-sized behavior patterns which are as simple as are a handful of definable molecules.

For this and other reasons several basic questions on chemosensory physiology were tackled first by an investigation of pheromone receptor cells, as was the case with the famous sexual attractant receptors of the silkworm (Schneider, 1957). Until now most of the promising approaches to problems on primary- and transduction processes in olfactory receptors have been undertaken in pheromone receptors (Kaissling, 1971, 1974, Kafka and Neuwirth, 1974).

Unfortunately we are still far away from an understanding of the events occurring between the arrival of an olfactory molecule at the receptor membrane and the arrival of nerve impulses at motor centers governing the activity of the animal. Already at the receptor level there is only a vague mosaic of data from different experimental animals. At the central nervous level, we are rather in the very beginning of the investigation. Therefore, only a very general picture of insect olfactory neurophysiology can be given together with a few patches of more detailed knowledge, and only a few data with special reference to pheromones.

Since there are recent review on this topic (Kaissling, 1971, Boeckh et al., 1976) only a selection of results and viewpoints is presented which is chosen in order to stimulate discussion rather than to offer a complete picture of today's knowledge.

Insect olfactory receptor cells are found in a variety of hair- or plate-like cuticular sensilla which are located mainly on the antennae. The stimulus, i.e. molecules of certain compounds, reach the sensitive processes of the receptor cells (the dendrites) via pores or slits in the hair wall (Fig. 1). The primary reaction of the receptor cell presumably starts with an interaction between the odor molecule and specific acceptor molecules of the cell membrane. Only molecules which "fit" the acceptors of the membrane can elicit a reaction. According to Kafka (1974) and others, this fit is brought about by a certain spatial distribution of atoms and charges in the odor molecule (chain length, location of functional groups or multiple bonds) which enables the development of weak interactions to certain loci of the acceptor (Fig. 2). These interactions can take place if the molecule reaches a certain position opposite the acceptor. The interactions cause molecular changes in the receptor cell membrane which in turn lead to a change in ion permeability of the membrane (Fig. 3): a depolarization (or hyperpolarization) occurs which is called a receptor potential. The receptor potential spreads to a specialized part of the cell, the generator region, where nervous impulses are generated (or suppressed) under the influence of the receptor potential. The impulses are the signals to the central nervous system. Receptor potentials and impulses can be recorded by means of extracellular electrodes (Fig. 4).

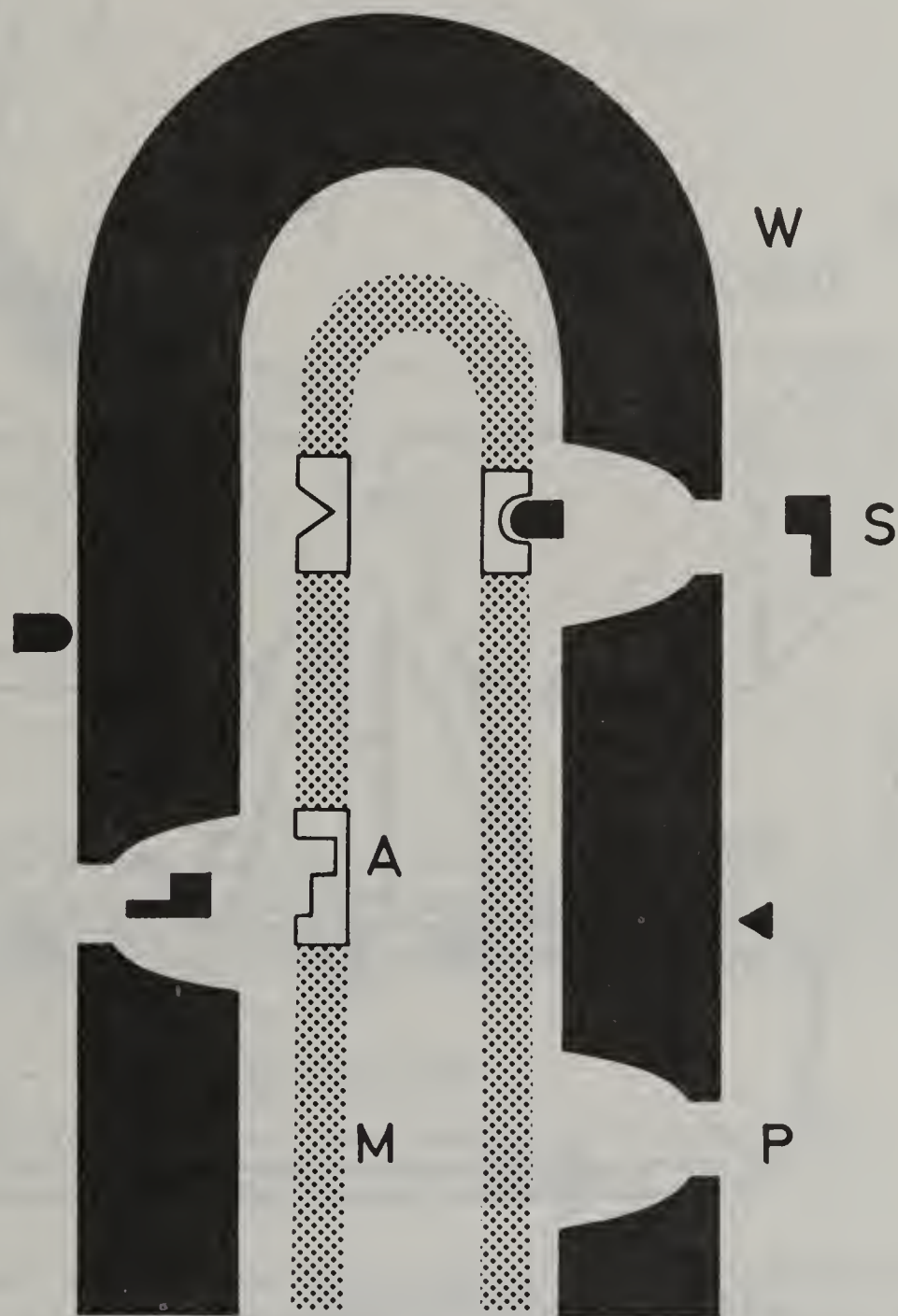


Fig. 1. — Part of an insect olfactory sensillum. Odor molecules (S) reach the cuticular hair wall (W), and, via the wall pores (P), the acceptors (A) of the membrane (M) of the receptor cell dendrite.

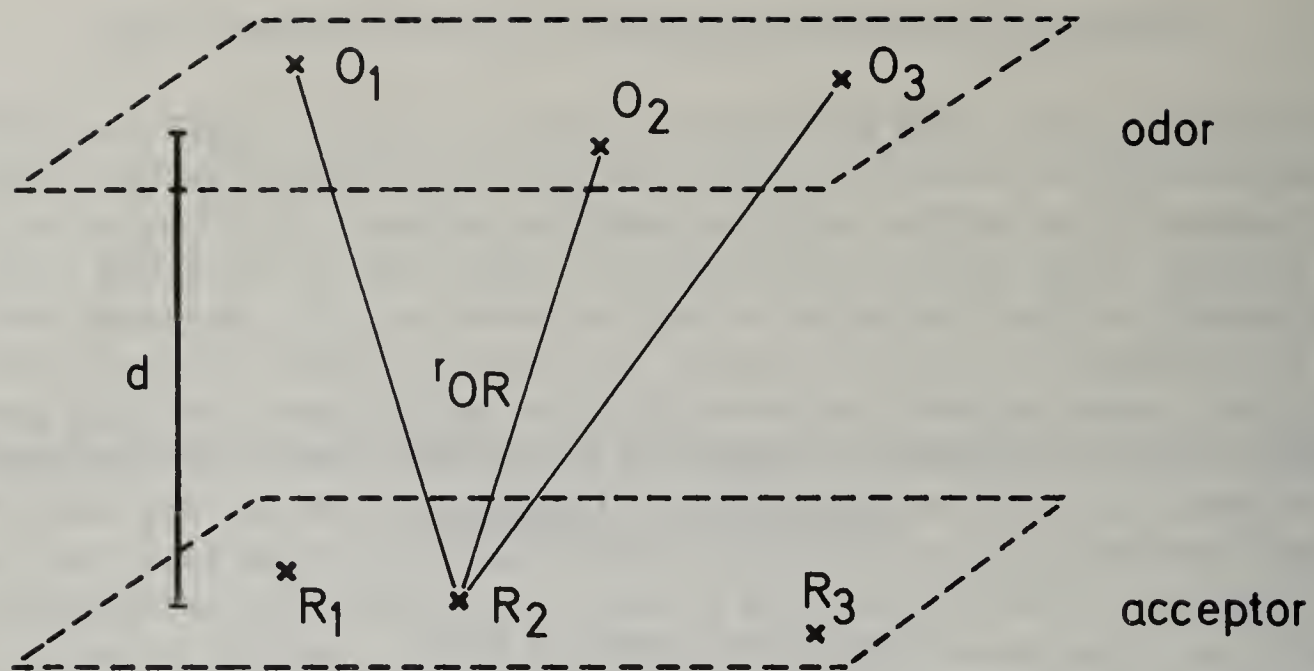


Fig. 2. – Interaction between an odor molecule and an acceptor in the dendritic membrane of an olfactory receptor cell. At a given distance (d) and with certain geometrical positions of the molecule, weak intermolecular forces (r_{OR}) develop between certain essential regions of the odor molecule ($O_1 \dots O_3$) and the acceptor ($R_1 \dots R_3$). The model is derived from calculations based on response spectra of receptor cells. The “fits” of different molecules were tested in terms of receptor activity. (Modified from Kafka, 1974).

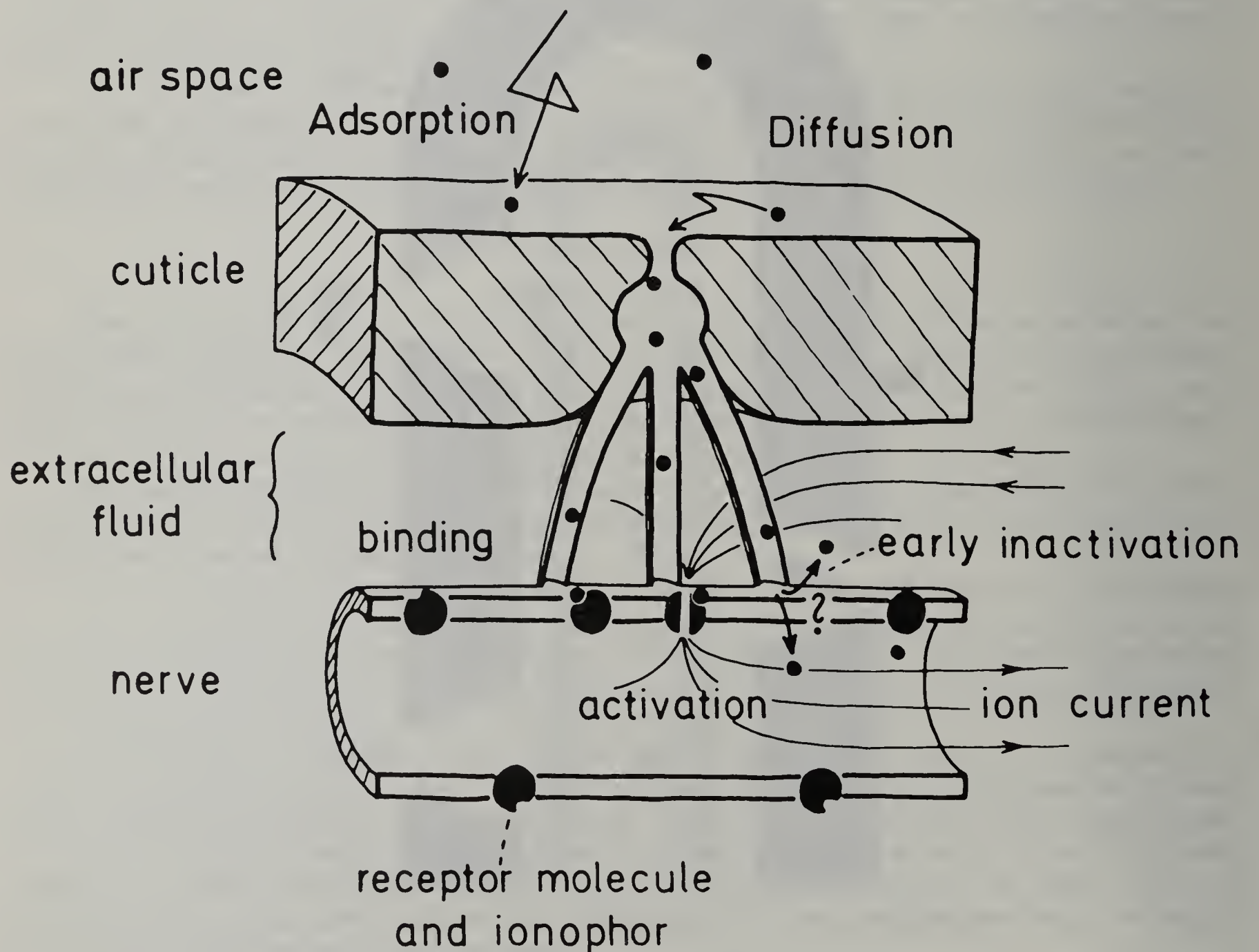


Fig. 3. – Model of primary and transduction processes at a pheromone receptor cell of the silkworm. (After Kaissling, 1974).

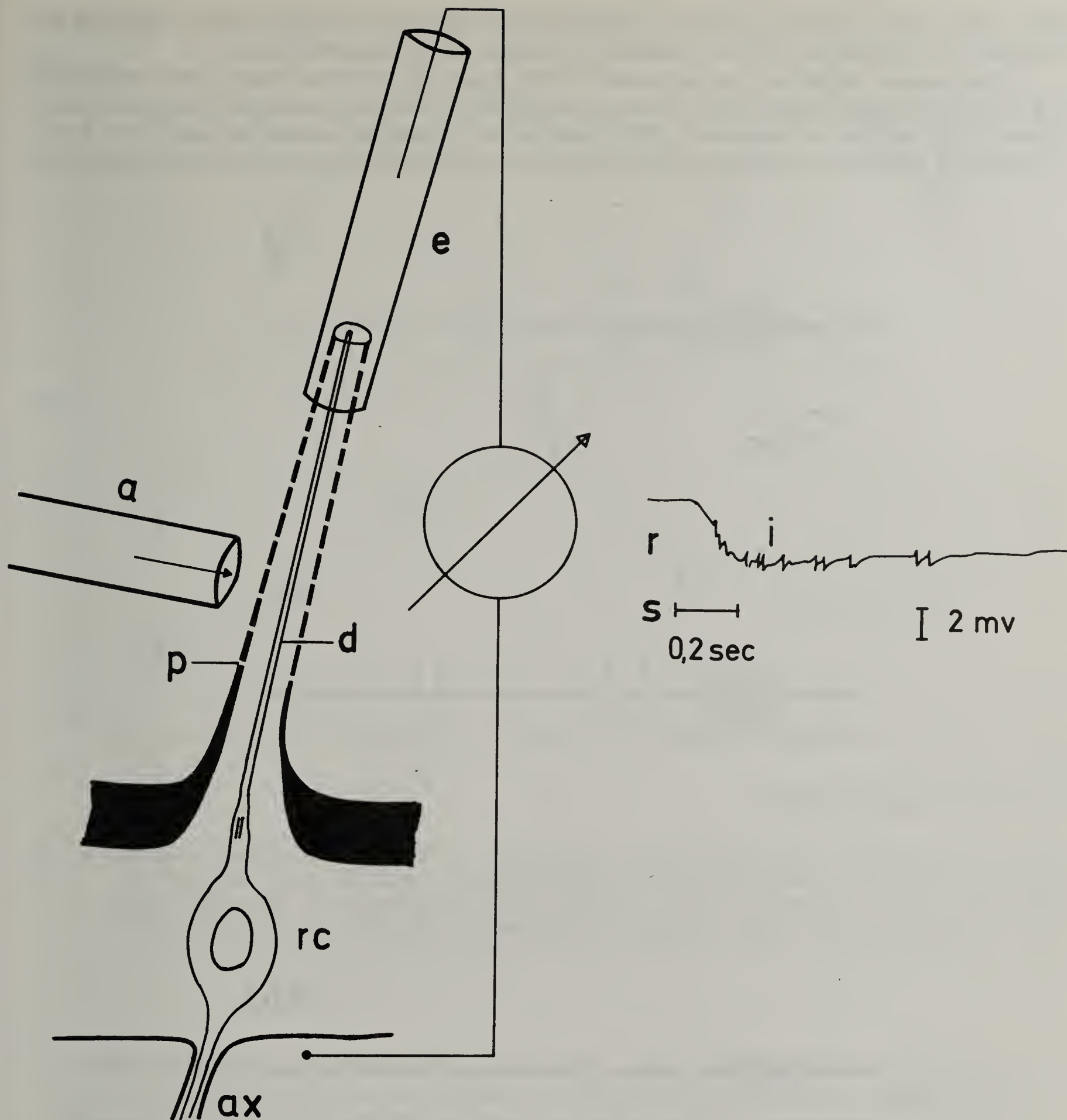


Fig. 4. — Kaissling's arrangement for recording receptor potentials and nerve impulses from an individual sensillum. The hair is cut, and the potentials are recorded via a capillary electrode (e) which is slipped over the cut end. The stimulus is given via a small outlet (a) near the hair. Ax, axon of receptor cell (rc); d, dendrite; i, nerve impulses; r, receptor potential; s, stimulus time. (Modified from Kaissling, 1974).

Specificity of Receptors (see Kaissling, 1974, Kafka, 1974, Priesner et al. 1975, Sass, 1976)

In some "simple" cases, as in the pheromone systems for sexual attraction of the silkmoth, only one compound (10-trans, 12-cis+hexadecadienol) is a highly potent stimulus which, at very low concentrations, elicits the full searching behavior of the male. It is effective at a concentration (about $3 \cdot 10^3$ molecules/cm³) where only about 1% of all pheromone receptor cells of the male are hit by one molecule each (Kaissling and Priesner, 1970). In other cases, like in the Saturniid moth *Antheraea polyphemus*, the sexual attractant gland of the female produces at least two different compounds which are of maximal effect as an attractant for the male only in a certain ratio (Kochansky et al.

1975). Each of both substances elicits a response only in one type of receptor cell, so that with the full gland odor two receptor cells are activated to a certain relative degree (Fig. 5).

Other natural odors such as the odors of fruit, meat etc. consist of many more compounds. Here the question arises whether these odors are recognized by a single characteristic compound or by a characteristic mixture of compounds. This question was investigated in detail by Sass (1973, 1976) in *Periplaneta americana*. In this insect, the olfactory receptor cells on the antennae are grouped into

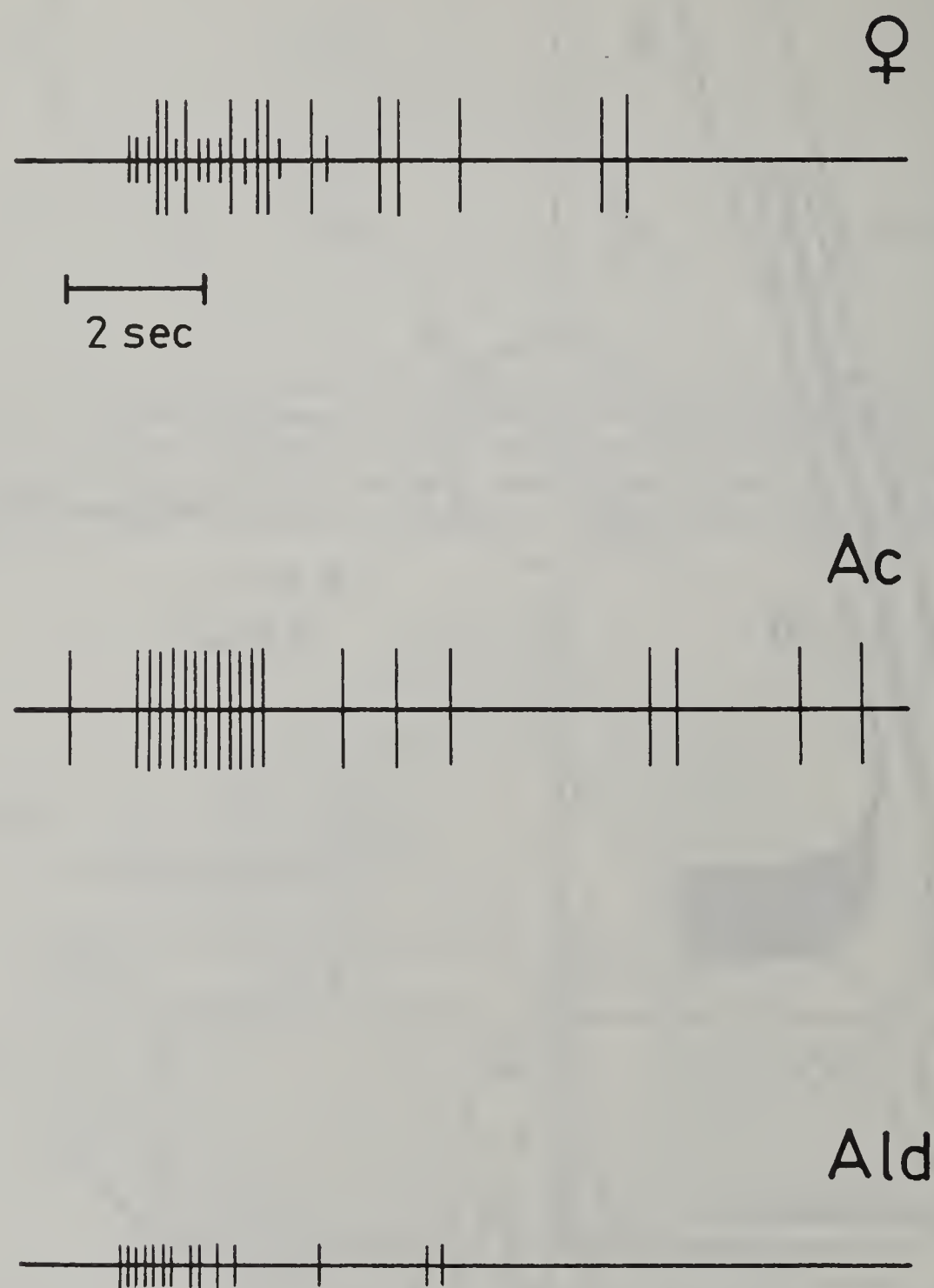


Fig. 5. – *Antheraea polyphemus*. Simultaneous recording of responses of two receptor cells in an antennal hair to the female sexual attractant and its components. ♀, female gland, Ac, trans-6-cis-11-hexadecadienylacetate, Ald, the corresponding aldehyde (stimulus strength = 10^{-3} μ g on filter paper). Note that both cell types (impulse amplitudes) react to the gland while each component is effective only to one cell type. Stimulus time marked by time scale. (Modified from Kochansky et al. 1975).

a limited number (about two dozen) of receptor types. All members of a given type react with the same specificity to a certain series of compounds, which makes up the so-called odor spectrum of that type. The spectra of different types overlap considerably, i.e. there are several compounds which are effective stimuli for more than one cell type. In all cases, the reactions to different compounds of the spectrum are graded, i.e. a few compounds are highly effective while others are of lesser effects (Fig. 6).

Natural odor sources like banana or apple for example contain up to several hundred volatile compounds as alcohols, esters, terpenes, many of which are effective stimuli for the receptor cells of *Periplaneta*. Each fruit contains several compounds out of the spectra of several receptors. Therefore it is not surprising to find reactions of more than one receptor type to the stimulus of a given fruit.

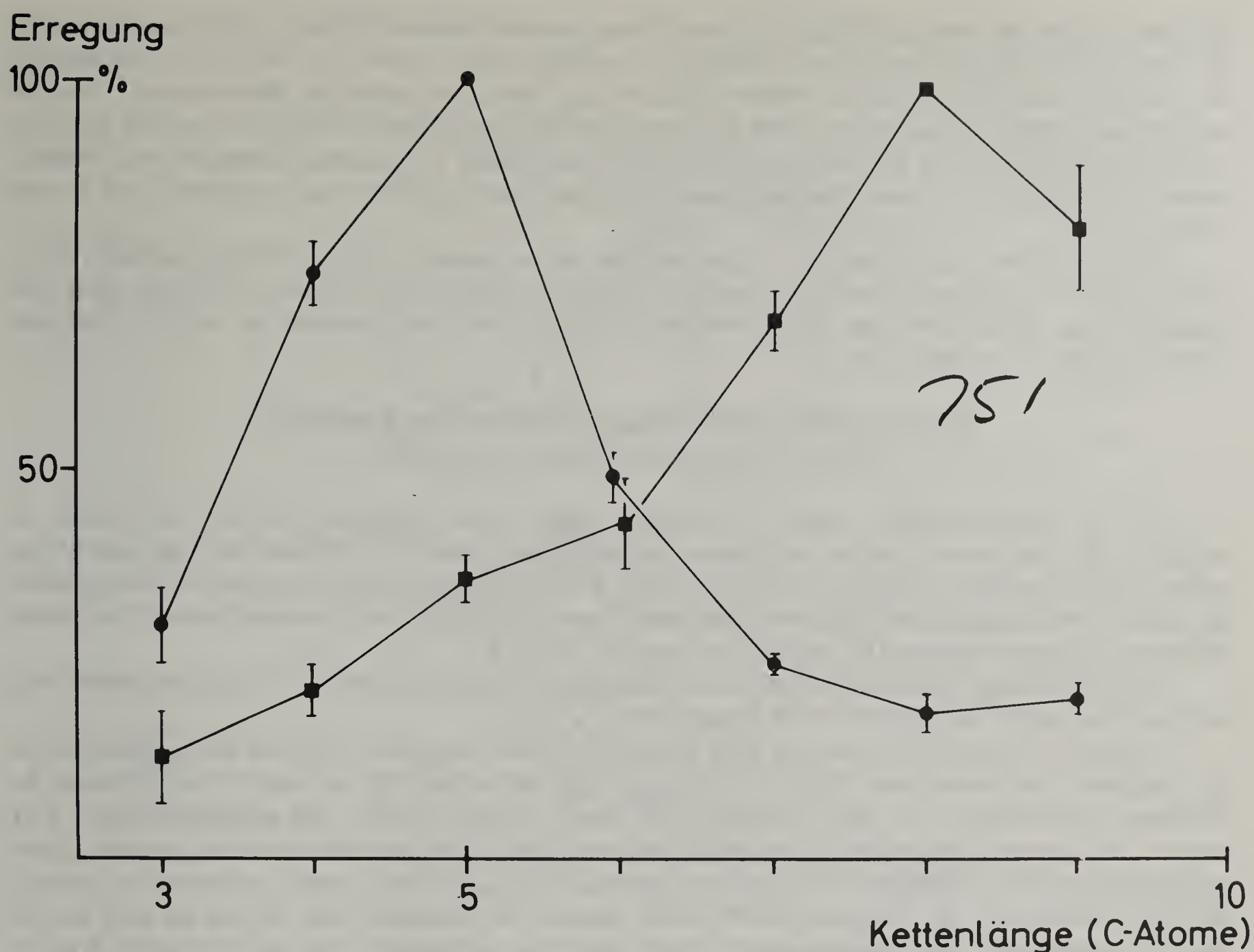


Fig. 6. — *Periplaneta americana*. Section of the odor spectra of two different types of olfactory receptor cells. Abscissa, chain length of aliphatic alcohols between C 3 (=propanol) and C 10 (=decanol). Ordinate, impulse frequency in % of maximum excitation. Means of 7 cells of the pentanol receptor type (left hand curve with maximum excitation with pentanol, C₅) and of 8 cells of the octanol type (maximum excitation with octanol, C₈). Stimulus concentration is at 10⁴ fold dilution. (From Sass, 1973).

Table 1.— *Periplaneta americana*. Odor spectra of 9 receptor cell types (arabic numbers) in 5 types of antennal sensilla (roman numbers). ++, excitation higher than 50% maximal impulse frequency; +, between 25 and 50% maximal impulse frequency; 0, no response. (After data of Sass, modified from Boeckh et al. 1976).

Sensillum type receptor cell nr.	I		II		III		IV		V
	1	2	1	2	1	2	1	2	1
banana	++	0	+	+	++	0	+	+	+
apple	++	0	++	+	++	0	+	+	+
lemon	+	0	+	+	++	0	++	+	+
orange	++	0	+	+	++	0	++	0	+
bread	++	0	+	+	+	0	+	+	+
fresh meat	++	0	+	+	+	0	+	+	+
old meat	+	+			+	+	0	0	++
cheese	+	+	0	0	0	+	0	0	++

But there is also an overlap in the occurrence of compounds between different fruit types. Therefore the reaction of a given receptor type depends (1) on the relative content of effective compounds in the complex odor, and (2) on the relative effectivity of these compounds for the receptor. From the experimental results it can be seen that different foodstuffs are effective stimuli for a whole series of receptor cell types, but in a graded and differential way (Table 1). Thus each complex odor elicits a certain and characteristic reaction pattern in the cell population rather than a reaction only in one receptor type.

This "cooperation" of receptor types enables the organism to form different patterns for a great number of different complex stimuli by a limited number of receptor cell types. Here the question arises as to how the central nervous system reads these patterns in order to evaluate parameters like olfactory quality.

Anatomy of the Central Olfactory Pathway (see Ernst et al. 1976; for review, see Boeckh et al. 1976)

In the central nervous system the coded message about stimulus quantity and quality is evaluated and integrated together with other processes which govern the actions and reactions of the animal. Our knowledge about the neuroanatomical and neurophysiological properties of this network in insects is very limited. Only recently have more research groups started investigations of the central olfactory pathway in insects (for review, see Boeckh, 1976).

The anatomical results are based on investigations by light microscopy (silver impregnations), electron microscopy and experimental degeneration.

In general, the axons of receptor cells from the antennal flagellum terminate in the glomeruli of the ipsilateral deutocerebrum (Figs. 7, 8). Here, they are connected to higher order neurons. In *Periplaneta americana* more than 200,000 such axons terminate in the 125 glomeruli. About 570 neurons of a dorso-lateral region in the deutocerebrum send their processes into the glomeruli. Each glomerulus receives processes from several neurons, and each neuron sends processes to several glomeruli. Moreover, the receptor axons ramify within the glomeruli, and, as can be seen in the electron microscope, form connections to more than one postsynaptic element (divergent type of connection). Only 270 of the deutocerebral neurons (the relay neurons) send axons via the tractus olfactorio-globularis towards other centers of the brain. Other deutocerebral neurons seem to function as local interneurons. There appears to be a great number of synapses in the glomeruli which do not serve as direct connections between receptor axons and relay neurons. These probably connect higher neurons with one another. From this and from other neuroanatomical studies it can be concluded that there are not only highly complicated "vertical" connections between many receptors and a few relay neurons for the transmission of signals from the periphery to higher centers, but also many "horizontal" connections between the different channels. The deutocerebral axons of the tractus olfactorio-globularis terminate in the calyces of the mushroom bodies as well as in the lobus lateralis protocerebri. In these regions the information from the antennal inputs is fed into the higher integrating network of the insect brain. It should be emphasized that until now it has been hardly possible to identify anatomically specific pathways for certain sensory modalities or qualities within the deutocerebrum. Only certain branches of the antennal nerve, carrying axons of mechanoreceptors from the basal antennal segments can be traced separately (Masson, 1973, Boeckh et al. 1976).

Activity of the Central Olfactory Neurons (for review, see Boeckh et al. 1976)

In central olfactory neurons the time course of response is much more complicated than in the receptor cells. In the cockroach, honey bee, or locust, for example, receptor responses generally consist of excitation while in central neurons excitation or inhibition, off-responses, and on-off-responses are found (Fig. 9). This enlarged vocabulary of central neurons does not only permit a better gradation of responses, but also indicates different polarities of connections (excitatory, inhibitory) between receptor cells and central neurons. Moreover, it indicates that a given central neuron receives inputs from receptor cells of different reaction types (above): If one compound causes excitation of the central neuron, and if an other compound causes inhibition, each of these compounds has to be effective for a different receptor type, both types being antagonistically connected to the central neuron (Fig. 10). Other basic modes of connections can be proposed on the basis of a comparison between responses of antennal receptor cells and of central neurons. One of

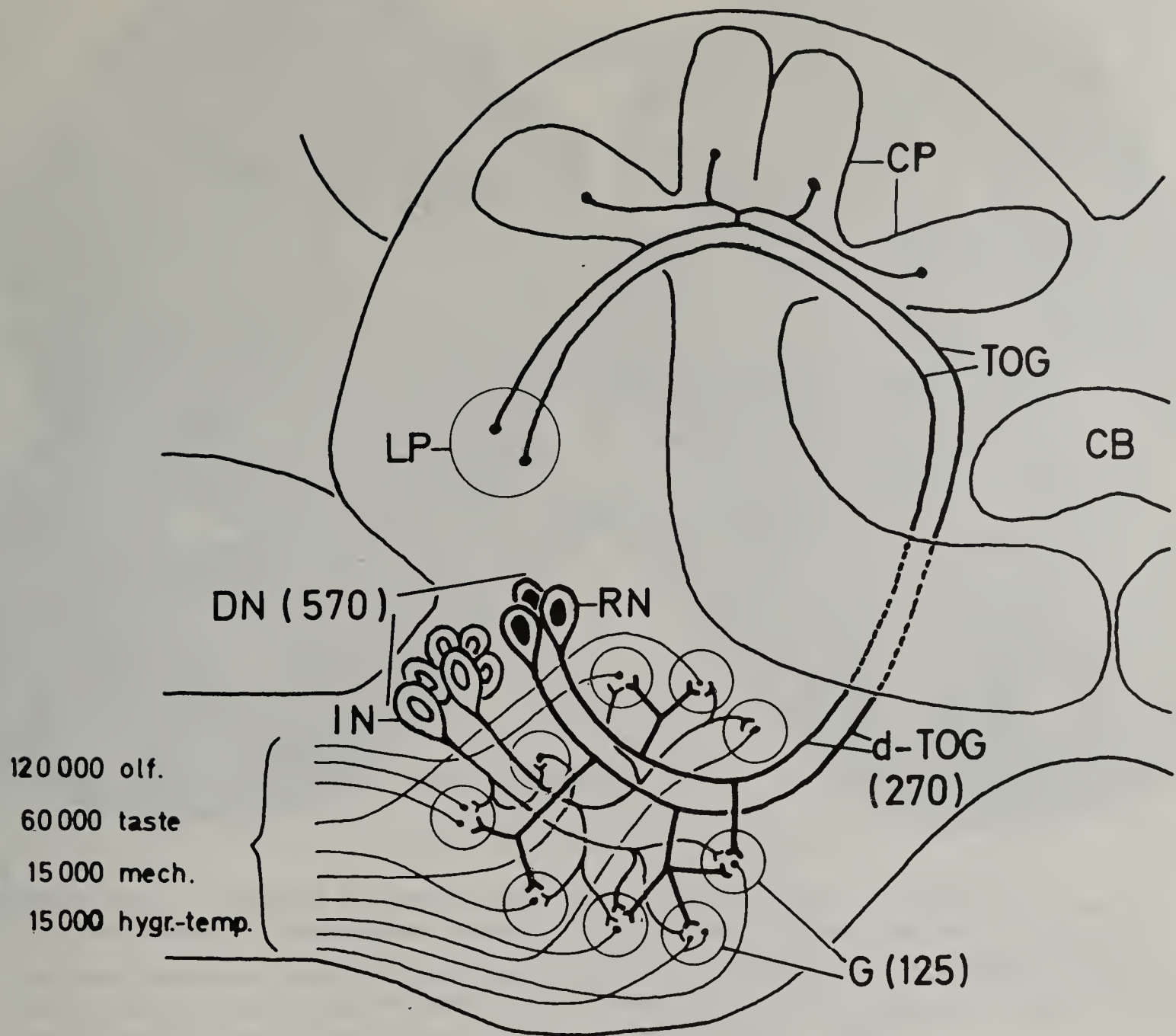


Fig. 7. — *Periplaneta americana*. Pathways of the inputs of receptor cells from the antennal flagellum. Diagram derived from silver impregnations and experimental degeneration studies. About 210,000 axons from different receptors (left hand side) arrive at the deutocerebral glomeruli (G). Hygr.- temp., receptors for humidity and temperature; mech., mechanoreceptors; olf., olfactory receptors. Deutocerebral neurons (DN) send processes into the glomeruli, but only RN-neurons send axons also to protocerebral regions (CP, corpora pedunculata; LP, lobus lateralis protocerebri). CB, central body; IN, local interneurons; TOG, tractus olfactorio-globularis; d-TOG, deutocerebral bundle of the TOG. Numbers in brackets indicate numbers of neurons, fibers or glomeruli. (Modified from Boeckh et al. 1975).

these modes is called spatial convergence. This term means that a given central neuron is connected to receptor cells from several or all antennal segments (Fig. 11). Another type of connection, the modality convergence, occurs at a certain type of central neuron which not only responds to olfactory but also to mechanical stimulation of the antenna. Since such a multimodality is not known in any receptor cell of the antenna, this effect can only be achieved by a convergence of inputs from different types of receptors at this type of neuron (Fig. 12).

The Response of Deutocerebral Neurons to Antennal Stimulation

Most experiments on deutocerebral neurons in insects have been performed with *Periplaneta americana* (Yamada, 1971, Boeckh, 1974, Boeckh et al. 1975, Waldow, 1975). Investigations on blowflies (Mimura, 1969), ants (Masson, 1973) and honeybees (Suzuki and Tateda, 1974) were not oriented especially towards problems of the processing of olfactory receptor inputs. According to their reactions to antennal stimulation, three major types of neurons can be discriminated in the cockroach deutocerebrum: Monomodal olfactory (type I), monomodal mechanosensory (type III), and multimodal (type II) neurons. A highly simplified list of their response characteristics is given in Table 2. The anatomical identity of these neurons has not yet been clarified. The reactions of type III neurons are simple to explain. These cells respond to mechanical stimulation of the antenna which occurs during bending, fluttering in an air stream, short touch or brushing. Antennal receptors for these stimuli are very probably companiform sensilla in the joints between the antennal segments.

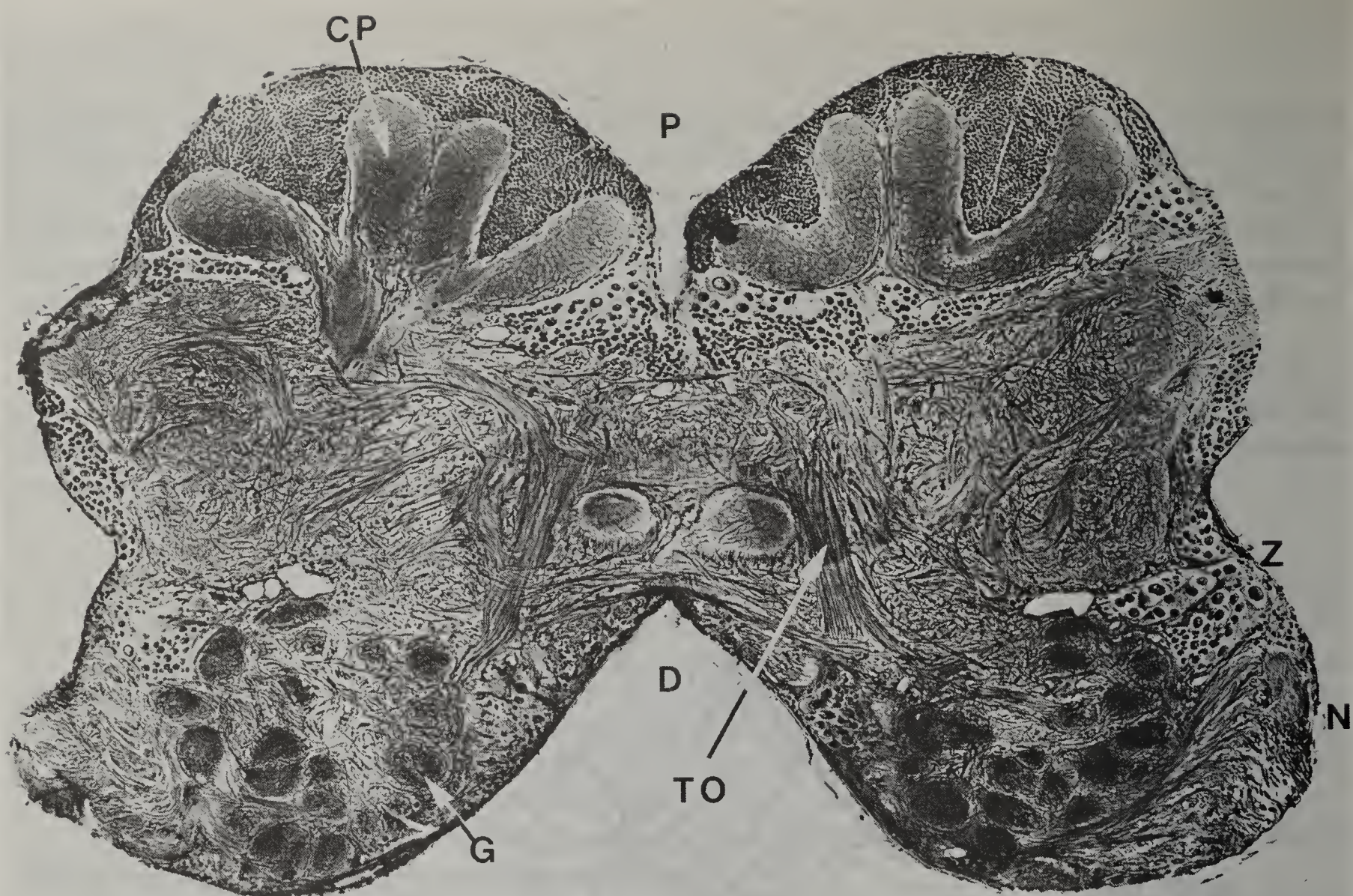


Fig. 8. — *Periplaneta americana*. Frontal section of the supraoesophageal ganglion. D, deutocerebrum with glomeruli (G) and deutocerebral neurons (Z). CP, corpora pedunculata; P, protocerebrum; TO, tractus olfactorio-globularis. (From Boeckh et al. 1970).

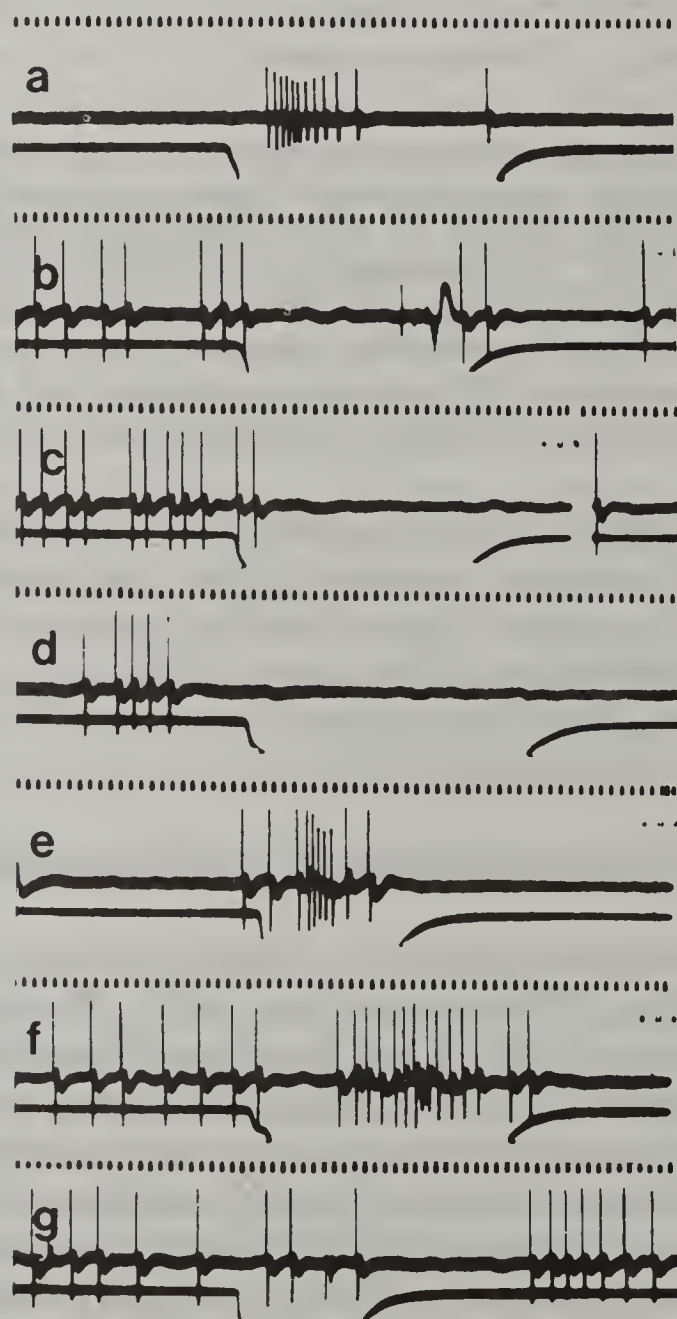


Fig. 9. — *Locusta migratoria*. Vocabulary of a deutocerebral neuron. Reactions to an alcohol (a), aldehyde (b), fatty acid (c), aromatic compound (d), terpene (e), fruit ester (f), and grass odor (g). Time mark distance 20 msec, stimulus duration is shown on the lower beam. (From Boeckh, 1972).

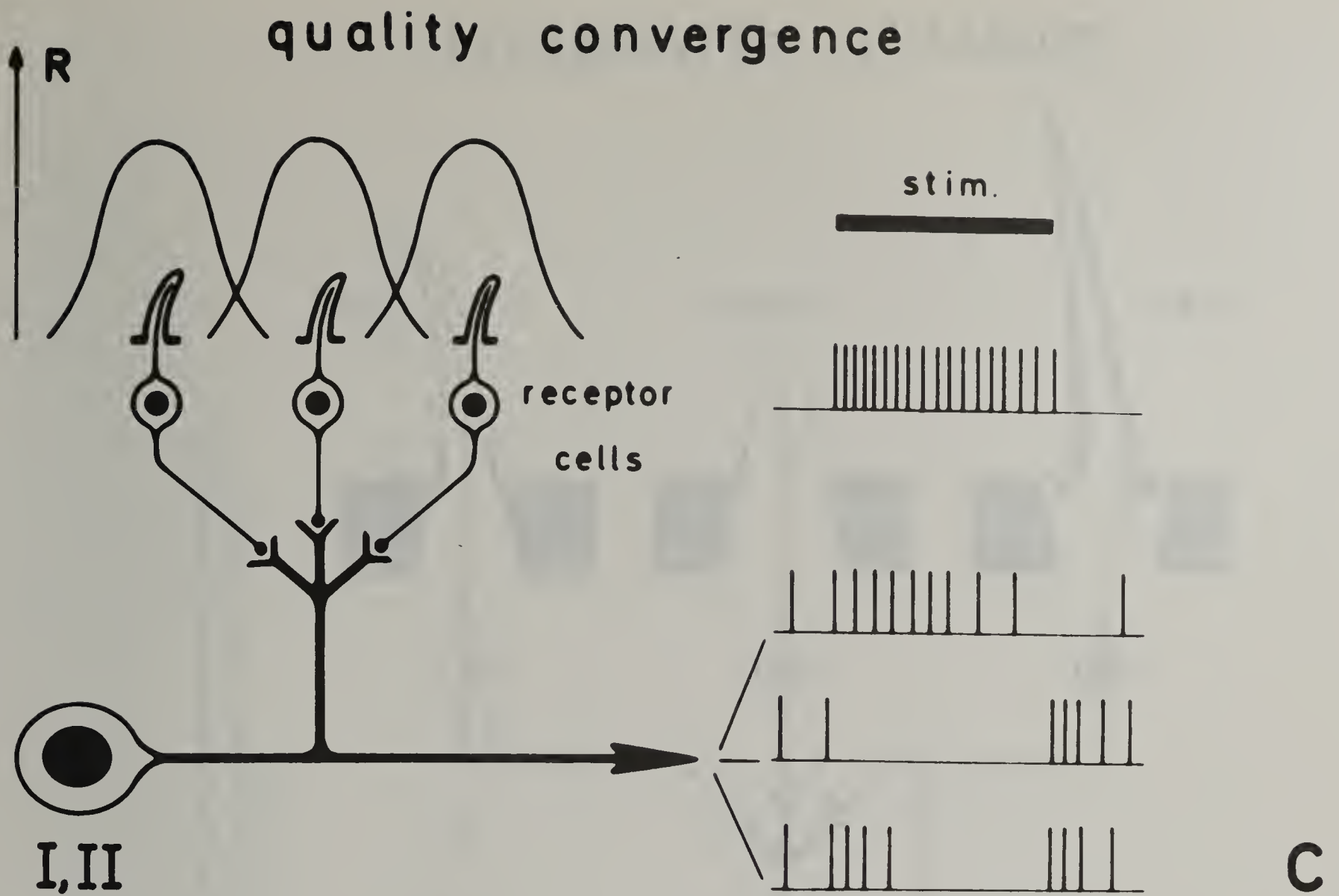


Fig. 10. — *Periplaneta americana*. Mode of connections between 3 receptor cell types with different odor spectra to a deutocerebral neuron. Receptor cells react to a stimulus (stim) by increase of impulse activity, the vocabulary of the central neuron is more diverse. (From Boeckh et al. 1975).

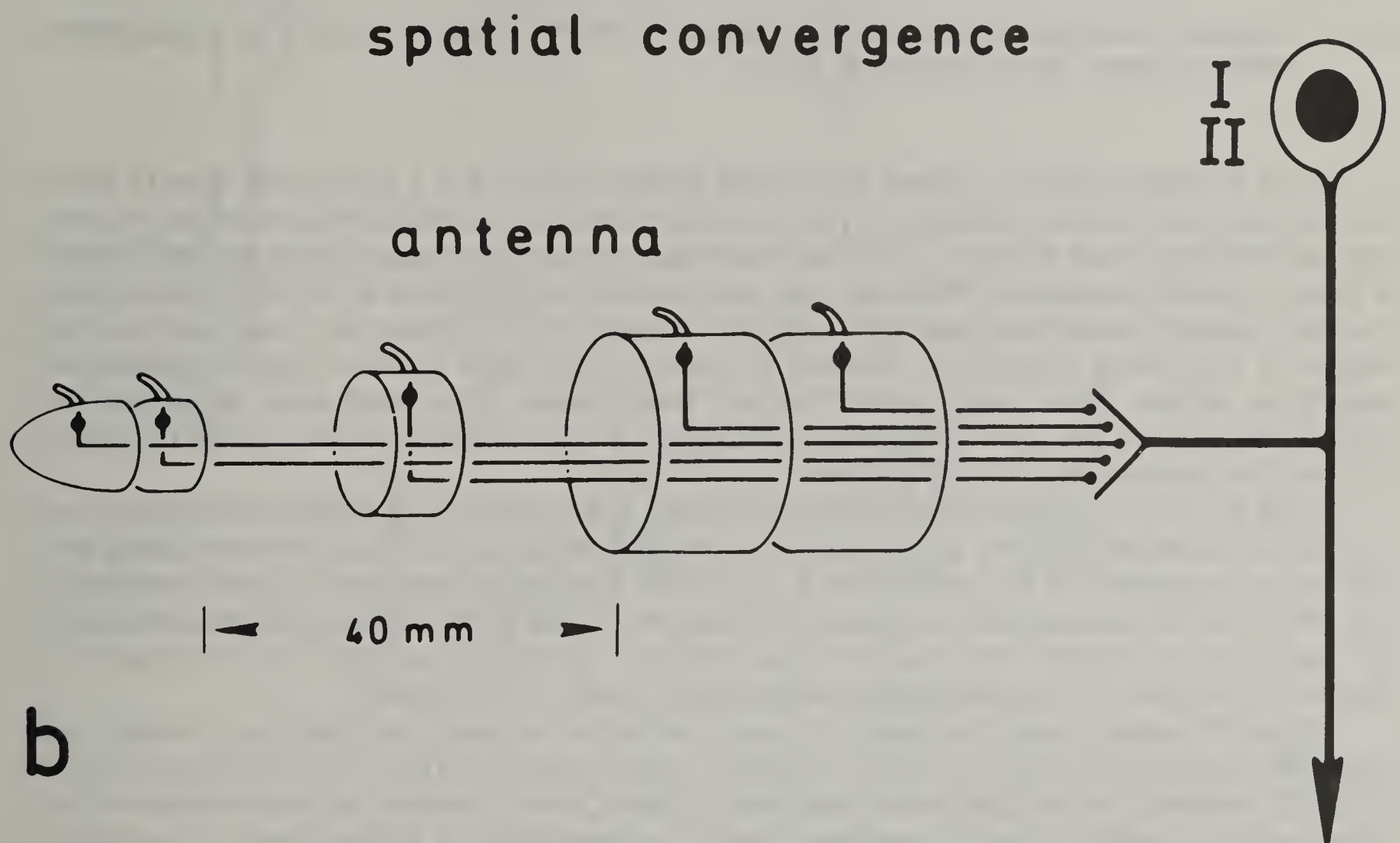


Fig. 11. — *Periplaneta americana*. Spatial convergence of receptors from different sections of the antenna to a deutocerebral neuron of type I or II. (From Boeckh et al. 1975).

modality convergence

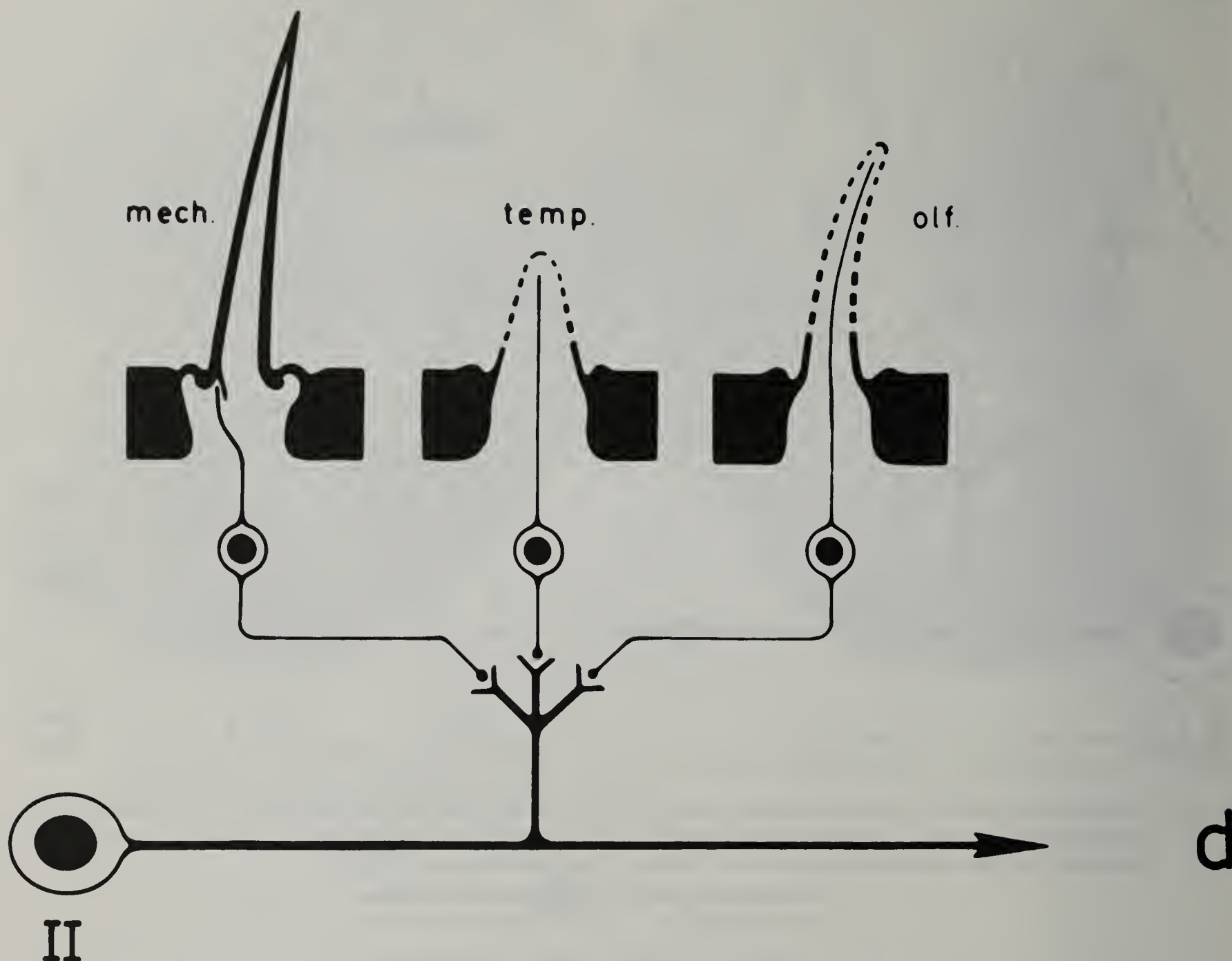


Fig. 12. — *Periplaneta americana*. Convergence of receptors of different stimulus modalities on a deutocerebral neuron of type II. (From Boeckh et al. 1975).

Type I neurons can be grouped into a well defined type Ia and a preliminary type Ib which possibly comprises different subtypes. Type Ia is characterized by its well defined responses to odors from cockroach colonies which are collected from cages containing groups of males or virgin females or larvae or mixed populations (Waldow, pers. communication, Boeckh et al. 1976). Odors of virgin females or young females were especially effective. Yamada (1971) reports that some deutocerebral neurons in *Periplaneta* were highly activated by extracts from virgin females. Type Ia neurons also respond to extracts from male colonies but to a lesser degree. Since there were no isolated nor purified pheromones and other “cockroach substances” at hand during this investigation, the exact effect of these substances could not be tested.

Type Ia neurons respond also to odors of lemon, and orange, and to several compounds as are alcohols and terpenes (Waldow, pers. communication; Boeckh et al. 1976) the latter not being very effective in comparison to the fruit odors. It is not clear whether the responses of type Ia neurons to fruit odors and to the compounds originate in a sensitivity of the corresponding pheromone receptors for these odors or whether other receptor types feed into the type Ia neurons. The odor spectra of pheromone receptors are not sufficiently characterized or such considerations.

Type Ib neurons never responded to colony odors but in many cases they were strongly and specifically excited by certain fruit odors and also certain compounds (Fig. 13). The reaction spectra of type Ib neurons are not alike, but in most cases alcohols, esters, terpenes and other substances out of the spectra of certain receptor types were found to be most effective. In many cases the sensitivity for odors from foodstuffs (fruit, meat, etc.) was very high, often only a single of these complex natural odors was found to be markedly effective. The odor spectra of type Ib neurons comprise

Table 2.— *Periplaneta americana*. Response characteristics of deutocerebral neurons. alc., alcoholic compounds; ban., banana; lem., lemon; or., orange; terp., terpenes.
(Modified from Boeckh et al. 1976).

Stimulus modality		olfactory						thermal	mechanical
Neuron type (response vocabulary)		colony odors	food			alc.	terp.	fatty acids	amines
			or.	lem.	ban.	bread			
I	unimodal olfactory (on; on-off)								
		a)							
		b)							
II	multimodal (on; on-off; off; inhibition)								
III	unimodal mechanosensory								

odors from the spectra of several receptor cell types but in no case was a complete conformity between the spectrum of a central neuron and an individual receptor type ever found.

Type II neurons (Waldow, 1975) respond not only to odorous stimuli but also to mechanical and thermal stimulation of the antenna (above). Similar to type Ib neurons, they never responded to colony odors, but did to odors of different fruits, cheese, meat and other foodstuffs, as well as to a wide variety of odorous compounds from the spectra of different receptor types. A significant departure from the type Ib neurons is a marked response to amines and fatty acids in the type II.

In type II the odor spectra vary from the neuron to the other.

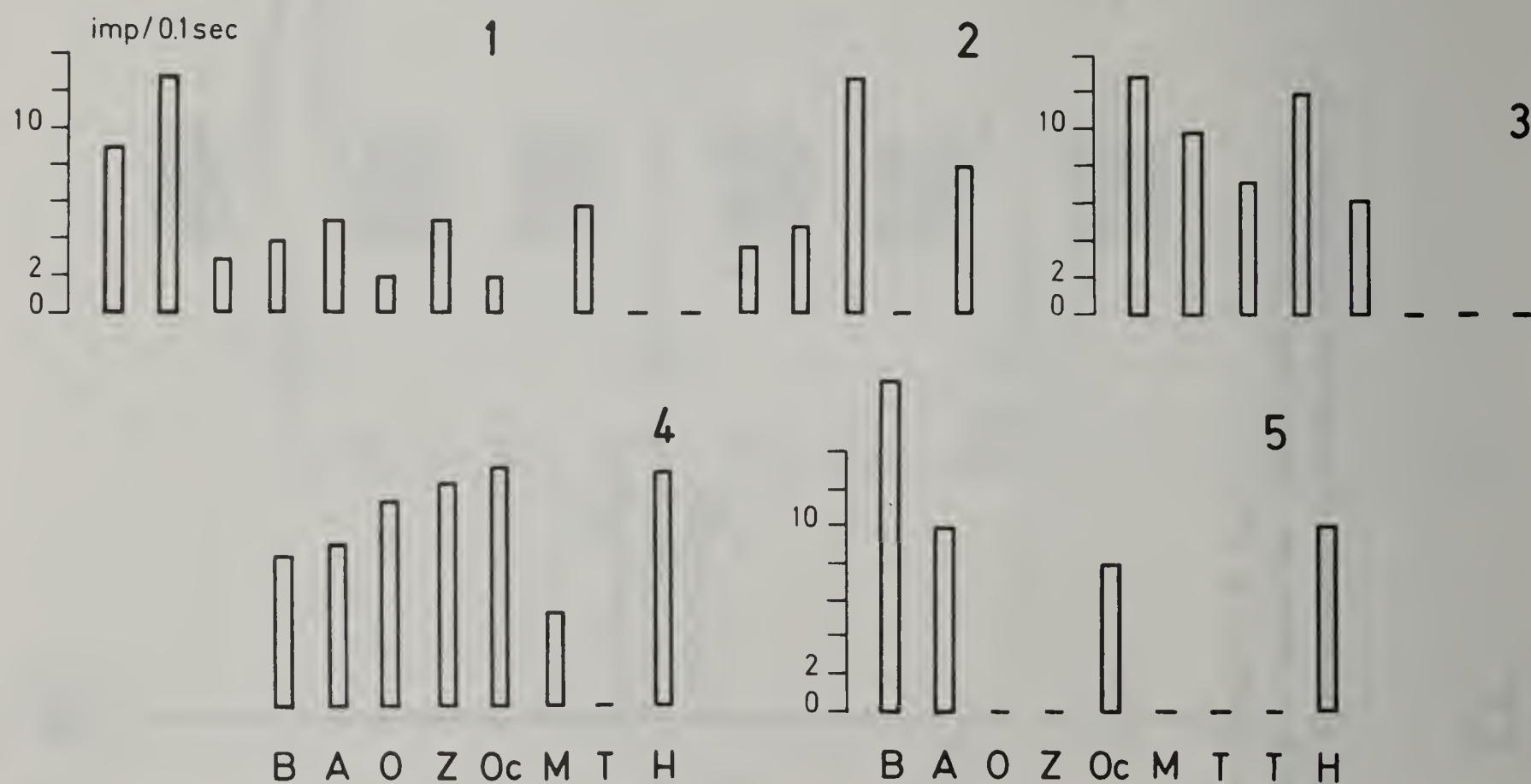


Fig. 13. – *Periplaneta americana*. Reactions of 5 type Ib neurons in the deutocerebrum to different odors: A, apple; B, banana; H, hexanol; M, 3-methyl-butanol; O, Octanol; T, terpeneol; Z, lemon. (From Boeckh et al. 1976).

Discussion

The complex responses of deutocerebral neurons to sensory stimulation of the antenna are difficult to understand. There seems to be some sort of specificity in the type Ia neuron for colony odors, but there are also significant responses to certain fruit odors. Moreover, there is no apparent qualitative specificity in these neurons for odors from female or male colonies. Since we know of the existence of two well defined and highly effective compounds in the female pheromone of *Periplaneta* (Persoons et al. 1976) it is surprising to find the corresponding central neurons only slightly more affected by odors from female colonies than from male colonies.

The additional responses to fruit odors in type Ia neurons might not confuse the central nervous system because if there are only colony odors in the environment Ib and II-neurons would not respond. If there are food odors and colony odors simultaneously present then differential excitation patterns of several populations of neurons could prevent confusion, because of the overlap between their odor spectra. The marked selectivity of several Ib- and II-neurons for odors of single foodstuffs offers a good possibility for an olfactory discrimination between such complex natural odors. However, an interpretation of these odor spectra of these neurons in terms of receptor spectra is difficult. There is no correspondence between any single receptor spectrum or a combination of such spectra and a central neuron spectrum. Therefore, we are left with two possible interpretations: (1) the receptors which feed into the central neurons have not yet been found. This means that none of the central neurons investigated is connected with one of the known receptor types which is very improbable. (2) There is a complicated interaction between the receptor inputs at the central neurons.

If we leave out possibility (1), then we have to search for an explanation of the spectra of the central neurons in terms of spectra of known receptor types. A quantitative investigation reveals that the relative sensitivity of many central neurons, especially in type Ib, for fruit odors seems much higher than for the single compounds tested (Fig. 13). Excitation levels of more than a hundred impulses per second are often achieved during stimulation with a fruit odor, while single compounds have much lower effects even in dilutions of 10^3 or 10^2 times (which is near saturation). In receptor cells, as in the pentanol type (Fig. 6), the odor of banana is about equivalent (in terms of impulse-frequency) to 3-methyl-butanol diluted 10^5 times. One could speculate now that, at the central neuron, the mixture of several or many odorous compounds in the fruit might exert a higher effect than a single compound, because the different compounds in the fruit are effective to several receptors which could add their effects in a nonlinear way at the central neuron input. A preliminary experiment with a very simple mixture reveals such an effect. A mixture of terpeneol and octanol each diluted $3 \cdot 10^5$ times is significantly more effective at the type Ib neuron than a ten times more concentrated solution of either one of the constituents (Fig. 14). Since nothing is known about the effect of such mixtures upon the receptor cells nor is it certain that both substances are effective upon two different receptors converging at the Ib neuron input, this result has to be considered a contribution to the discussion rather than a decisive proof in favor of the hypothesis.

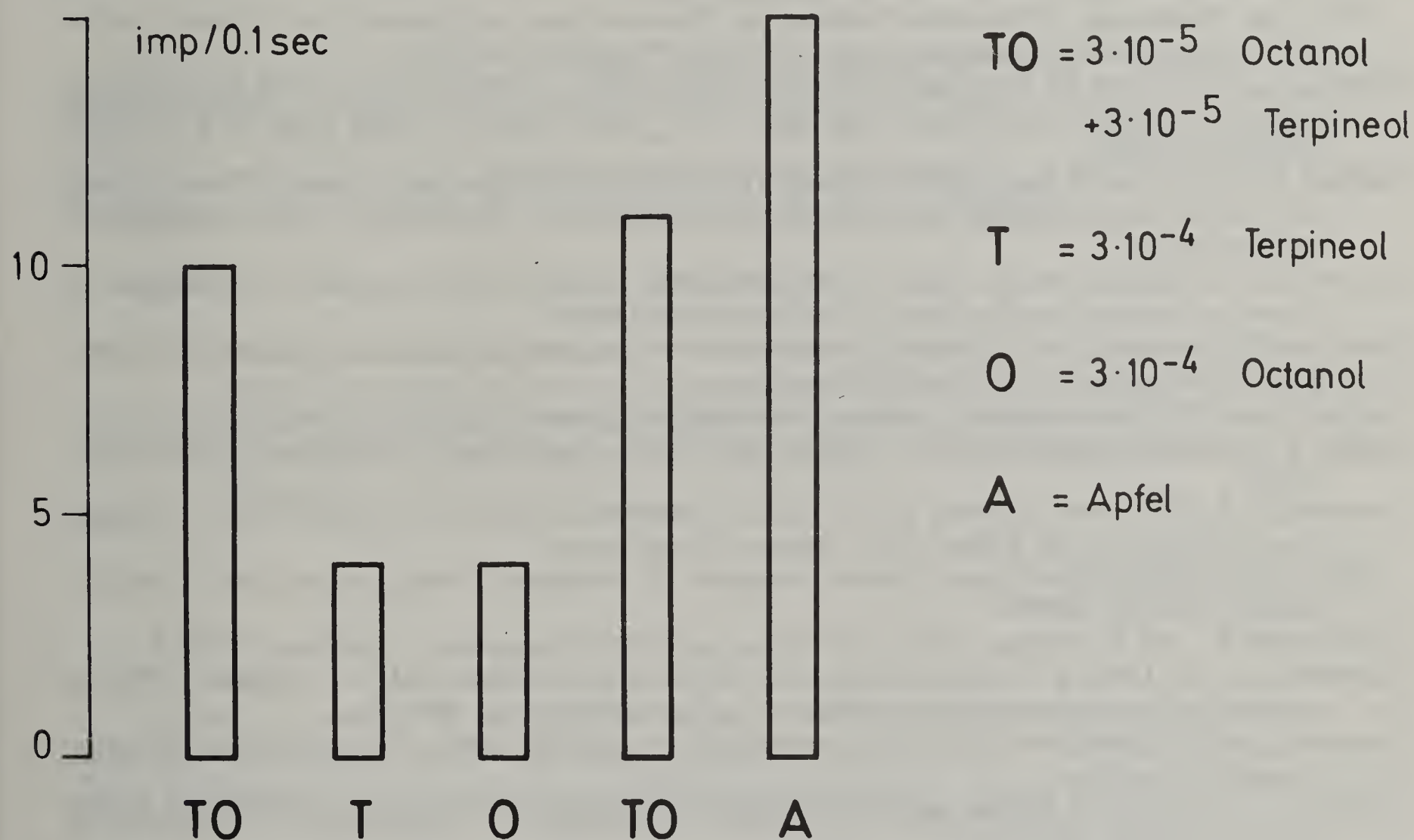


Fig. 14. — *Periplaneta americana*. Reactions of a type Ib neuron in the deutocerebrum to the odor of apple (A), and to two compounds given in mixture (TO), and separately (T,O). Stimulus strengths are given in relative concentrations. Note that in the mixture (TO) the compounds are more effective at a 10 times lower concentration than if given separately. (From Boeckh et al. 1976).

The functional significance of the multimodal neurons remains obscure. In most natural situations olfactory and mechanical stimuli (air currents, movements of the antennae) will simultaneously arrive at the antenna. Why this coincidence of sensory events is reflected in the activity of neurons at this level is unknown. It is remarkable that these neurons respond to odorants such as amines and fatty acids, which do not affect the other neuron types. In this way, there is at least a section of the total olfactory spectrum of the animal represented selectively in certain types of central neurons.

In sight of these data, our ideas about a neurophysiological basis of the processing of olfactory data in the nervous system become very vague. One can detect a certain specificity in certain neurons for certain odors, but there is also considerable overlap between the odor spectra of the functional types of neurons. In addition, our knowledge on receptor spectra is apparently not complete enough for an explanation of the spectra of central neurons. Moreover, we have to suspect that the central neuron spectra originate in nonlinear and complex interactions of receptor inputs. Finally, our information about the abilities of odor detection and discrimination is extremely limited in our best neurophysiological animal, the American cockroach. Other insects, as e.g. the honeybee are much better known in this aspect, but there are severe limitations for an application of neurophysiological methods in this insect.

Therefore, the data presented above should only be regarded as very preliminary results. It could only be demonstrated that it is possible to investigate central olfactory neurons of insects with neurophysiological and neuroanatomical methods. The function of these neurons for an evaluation of sensory input signals remains obscure.

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Arthropod Allomones: Chemical Effronteries and Antagonists

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ABSTRACT

The role of allomones in the biology of arthropods is discussed with reference to physical, chemical, behavioral, morphological, and biochemical adaptations which aid the arthropod during its escape from or resistance to a variety of foes. This discussion attempts to outline some fundamental problems in our approach to studying allomones, and also attempts to point out other lines of investigation which may enhance our understanding of the role of allomones.

Introduction

"There was a man born blind, who had several apprentices in his own condition. Their employment was to mix colors for painters, which their master taught them to distinguish by feeling and smelling. It was indeed my misfortune to find them all at that time not very perfect in their lessons, and the professor himself happened to be generally mistaken".

in A VOYAGE TO LAPUTA,
from GULLIVER'S TRAVELS
by J. Swift

Contrary to survival is the relentless attack of foreign organisms (pathogens, parasites, and predators). The defensive and/or offensive mechanisms to parry such biological depredations may occupy a noteworthy position in an organism's biology, encompassing major bodily commitments for the evolution of morphological, biochemical and/or behavioral traits. The primary focus of this article will be on biochemical traits, especially allomones, which enhance the survival of arthropods. The term *allomone* (Brown, 1968, Brown et al. 1970) defines "a chemical substance, produced or acquired by an organism, which when it contacts an individual of another species *in the natural context* (quoter's emphasis), evokes in the receiver a behavioral or physiological reaction adaptively favorable to the emitter." Also, this article is not intended as a comprehensive review of allomones, but will direct itself to selected aspects of allomones produced by arthropods. In this sense allomones are what are trivially called defensive compounds or chemicals.

As symptomatic of the scientific mushroom, data on arthropod allomones (primarily exocrine) have accumulated exponentially (comparing reviews; Maloeuf, 1938; Roth and Eisner, 1962; Weatherston, 1967; Eisner, 1970; Weatherston and Percy, 1970; Pavan and Dazzini, 1971). A modern catalogue of such chemical species would contain entries in the order of thousands, derived from the order of 1×10^5 of the number of arthropod species. Admittedly, by comparison with the documentations of "secondary" products of green plants (Gibbs, 1974; Hegnauer, 1963-1969), many of which have putative allomonal roles, the arthropod catalogue is scanty. However, the majority of

our scientific victories seem to entail the subjugation of the unknown to a chemical structure, after which our pursuit wains in view of information that this new chemical is offensive to a laboratory predator. Hence, it is a detriment that a library of the occurrence of “secondary” chemicals in arthropods is building at the expense of a paucity of cross-reference to the allomone’s overall potential as a modifier of the biological interface into which the allomonal producer insinuates itself. This interface is a spectrum of adversities — large and small predators, bacteria, fungi, viruses, nematodes, and a variety of parasites — in which allomones “in their natural context” may physiologically or behaviorally alter the antagonists.

Many descriptions of chemically mediated defensive-offensive interactions between prey and predator are anecdotal. This statement must not be construed as a denigration of biographical or chemical descriptions of arthropod allomones. I am certainly not diminishing the scientific excellence of the elucidation of the structure of nitropolyzonamine (Meinwald et al. 1975) as a defensive component of the secretion of the millipede *Polyzonium rosalbum*, nor the value of descriptions of the morphological and behavioral adaptations of various insects for escaping predators (Blest, 1957; Claridge, 1968; Cott, 1940; Edmund, 1972; Eisner, 1974b; Eisner, et al. 1964; Happ, 1968; Kendall, 1974; Noirot and Quennedey, 1974; Robinson, 1969; Ruiter, 1955).

The use of the word anecdotal is a remonstrance of the hope that future research on arthropod allomones will extend itself beyond description of the visible. For example, *p*-benzoquinones are famed as allomones of beetles and millipedes (Eisner, 1970) almost to the degree of fact as potent deterrents against predators. Out of the natural context, in laboratories, the potency of these chemicals can be demonstrated yet, from this frame of reference it can only be hypothesized that *p*-benzoquinones are effective deterrents. To surpass this anecdote it is demanded that the defensive system be considered as much in the natural context as possible. I am unaware of any field study to corroborate laboratory studies showing that the defensive liberation of *p*-benzoquinones contributes to survival. Also, because of our visual limitations it is difficult to be anecdotal about the possible influence of excreted *p*-benzoquinones on non-visible organisms. Hence, by field and laboratory investigation of the obvious and less obvious, it should be possible to progress from hypothesis to theory. Such a theoretical framework will not just account for the momentary contact between prey and predator, where the allomone is an effrontery, but also account for the perpetual contact between the prey with microorganisms and parasites, where the allomone may have long term antagonistic effects.

From this viewpoint, Brown’s term *allomone* can be scrutinized, and hence either approved, modified, or least likely rejected. It is to be remembered that we are all imperfect in our lessons, and for this reason our science (smelling and feeling) often blindly colors the world in a different hue.

Allomones as Chemical Effronteries and Antagonists of Predators

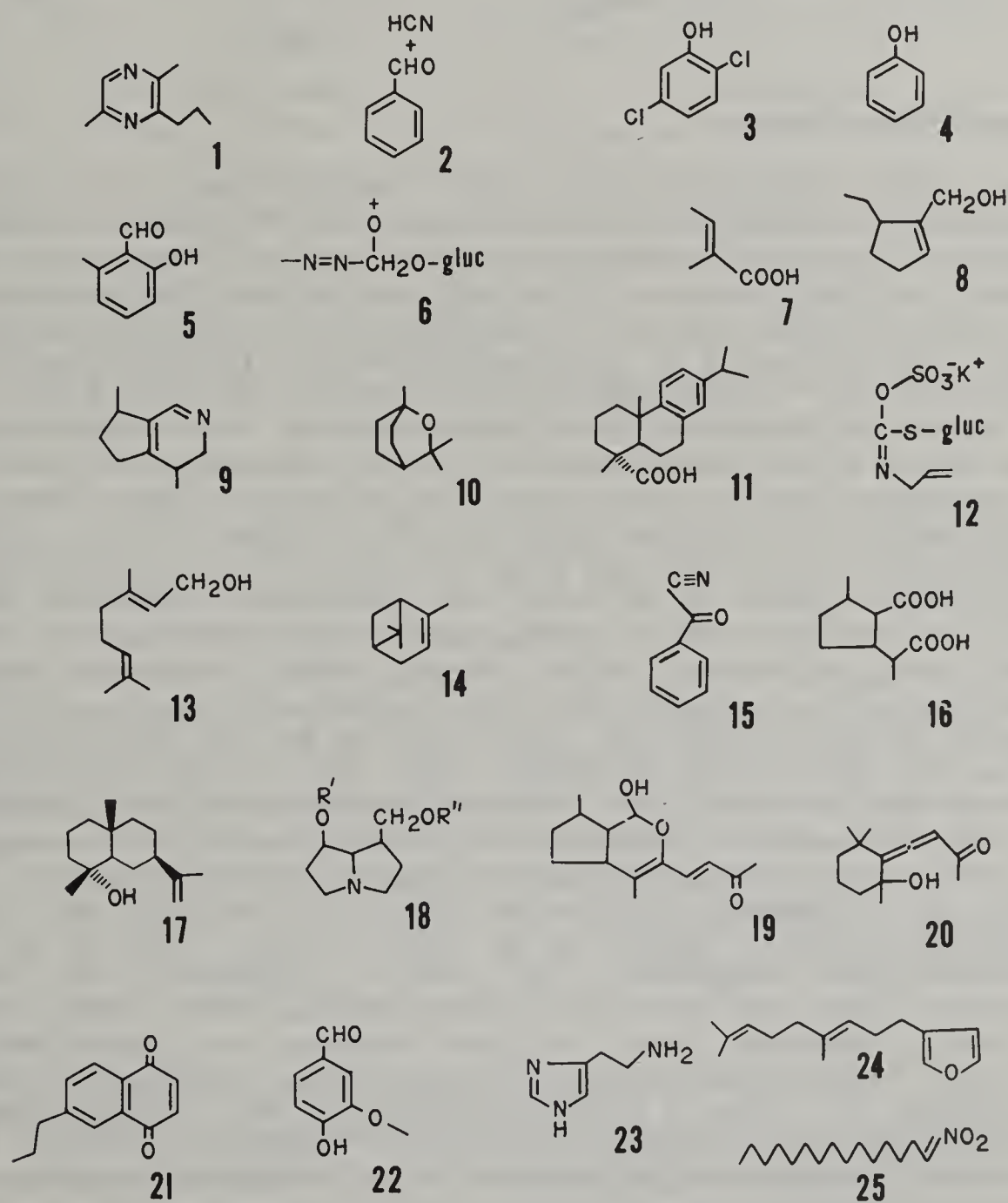
Chemical identity

The concept that arthropods utilize chemicals as a defensive mechanism against predators did not arise in the twentieth century. During the late 1800’s, in which strong opinions were voiced concerning the veracity of Batesian and Mullerian mimicry (see Cott 1940, Wickler 1968) in butterflies, it was eventually argued that unpalatable gaily-coloured butterflies (Slater 1877) derived their unpleasantness as larvae from the food plants. This hypothesis was not conclusively proven until studies with the Monarch butterfly (Brower and Brower 1964, Brower et al. 1968) demonstrated that larval feeding was responsible for the accumulation of offensive plant toxins in the adult butterfly. Historically, it was also realized that arthropods had glandular stores of defensive chemicals that probably originated in the bearer. As examples, it was known that a polydesmid millipede produced hydrogen cyanide (Guldensteeden-Egeling 1882), that formic acid emanated from the lepidopteran *Dicranura vinula* (Latter 1897), that the millipede *Polyzonium rosalbum* liberated a fluid with the distinctive odor of camphor (Cook 1900), and that the millipede *Iulus terrestris* exuded a benzoquinone (Béhal and Phisalix 1900). Earlier examples are cited by Roth and Eisner (1962).

With more modern techniques (e.g., nuclear magnetic resonance, mass spectrophotometry-gas liquid chromatography interfaces, and crystallography) our perspective of the biochemical capabilities of arthropods has been expanded considerably. I will make no attempt to catalogue all the natural arthropod products that have been implicated all allomones (see reviews by Eisner 1970, Weatherston

and Percy 1970, Pavan and Dazzini 1971). In perusing the following reviews it can be noted that the majority of reports of allomones involve identification of relatively simple organic molecules — alkanes; aliphatic acids, alcohols and their esters; cyclic and acyclic ketones and aldehydes; cyclic and acyclic monoterpenes; and simple benzoquinones and phenolics. In many instances the distribution of these chemicals is widespread throughout the living kingdom. There were few instances then of chemicals that were extremely rare in occurrence or unique to a given or few arthropods. For example the following chemicals were and still are considered of unique or rare occurrence; *p*-isopropylman-delonitrile glucoside (Pallares 1946), dendrolasin (Bernardi et al. 1967), 2, 3, 5-trimethyl-benzoquinone (Fieser and Ardao 1956), dihydromatricaria acid (Meinwald et al. 1968b), 1, 2-dimethyl-4(3H)-quinazolinone (Meinwald et al. 1966c), cantharidin (Meyer et al. 1968), and testosterone (Schildknecht et al. 1967a).

However, in the intervening years the identification of unique or rare products has increased greatly; assumably this is partly the result of a greater commercial availability of high resolution analytical equipment. The structures of many of these newly identified highly complex molecules are included in Fig. 1. This tabulation aims to impress upon the reader the diversity of chemical species primarily derived from the Insecta. The occurrences of many of these molecules in arthropods also constitute the only known examples of these chemicals in the biological kingdom, for example; nitropolyzonamine (45) (Meinwald et al. 1975); 6-butyl-naphthoquinone (21) (Tschinkel 1972); romallenone (20) (Meinwald et al. 1968a); 2-methylcyclopentanone (36) (Wheeler et al. 1975); prococcinelline II (26) (Pasteels et al. 1973); benzoyl cyanide (15) (Duffey et al. 1976b); 1-nitro-*trans*-1-pentadecene (25) (Vrkov and Ubik 1974); and 2, 6-dimethyl-3-ethyl-pyrazine (1) (Wheeler and Blum 1973). In view of the small number of total species of arthropods that have been examined for allomones (most of which are incomplete analyses identifying only major components) the future looks prosperous for the natural products chemist who will find fancy in arthropod defensive secretions.



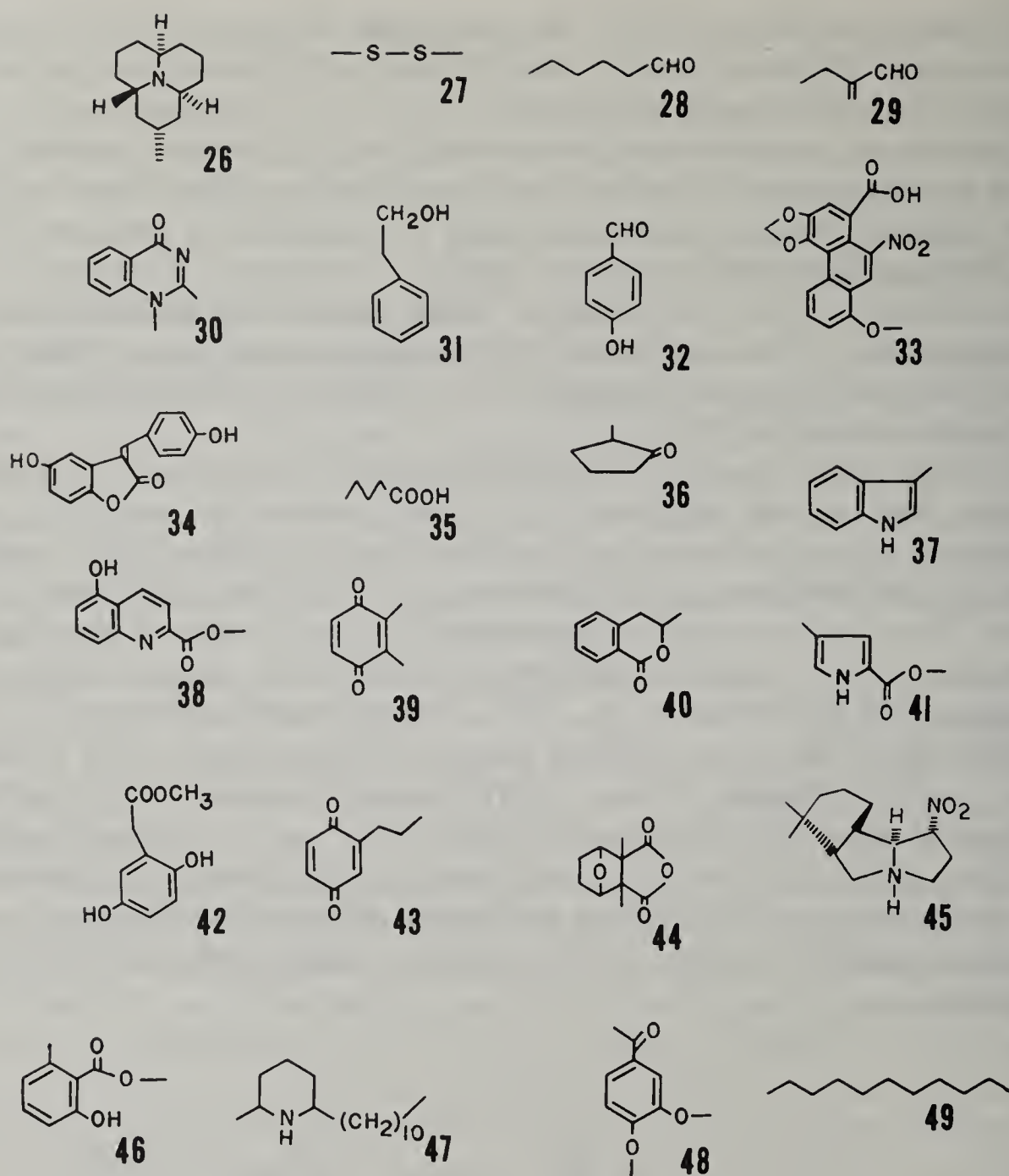


Fig. 1. —Some arthropod chemical defenses

¹2,6-Dimethyl-3-ethyl-pyrazine, Cavill and Houghton, 1974; Wheeler and Blum, 1973. ²Hydrogen cyanide and benzaldehyde, Blum et al., 1973a; Duffey et al., 1976b; Duffield et al., 1974; Eisner and Eisner, 1965; Eisner and Meinwald, 1966; Eisner et al., 1975. ³2,5-Dichlorophenol, Berger, 1976, 1975; Eisner et al., 1971a; Wood et al., 1975. ⁴Phenol, Aldrich et al., 1976; Blum et al., 1973a; Duffey et al., 1976a, 1976b; Duffield et al., 1974; Hoyt et al., 1971; Tschinkel, 1975a, 1972; Wood et al., 1976. ⁵2-Hydroxy-6-methyl-benzaldehyde, Moore and Brown, 1972. ⁶Cycasin, Teas, 1967. ⁷Tiglic acid, Benn et al., 1973; Moore and Wallbank, 1968; Schildknecht, 1971, 1970; Scott et al., 1975; Wheeler et al., 1970. ⁸(5-Ethylcyclopent-1-enyl) methanol, Moore and Brown, 1972. ⁹Actinidine, Bellas et al., 1974. ¹⁰1:8-Cineole, Schildknecht, 1970; Schildknecht et al., 1976. ¹¹Dehydroabietic acid, Eisner et al., 1974b. ¹²Sinigrin, Aplin et al., 1975; Rothschild, 1972. ¹³Geraniol, Blum et al., 1968a; Law and Regnier, 1971; Wilson, 1970; Wilson and Bossert, 1963. ¹⁴ α -Pinene, Eisner et al., 1974b; Moore, 1968. ¹⁵Benzoyl cyanide, Duffey et al., 1976b. ¹⁶Nepetalinic acid, Cavill and Houghton, 1974. ¹⁷Selin-11-en-4-a-ol, Eisner et al., 1971b. ¹⁸Pyrrolizidine alkaloids, Aplin et al., 1968; Edgar et al., 1973; Haber, 1975; Meinwald et al., 1971; Pliske and Eisner, 1969. ¹⁹Gyrinindone, Miller et al., 1975. ²⁰Rom-allenone, Meinwald et al., 1968a. ²¹6-n-Propyl-naphthoquinone, Tschinkel, 1972. ²²Vanillin, Aldrich et al., 1976; Ubik et al., 1975. ²³Histamine, vonEuw et al., 1967; Games and Staddon, 1973a; Rothschild, 1972. ²⁴Dendrolasin, Bernardi et al., 1967. ²⁵1-Nitro-trans-1-pentadecene, Vrkoc and Ubik, 1974. ²⁶Prococcinelline II, Pasteels et al., 1973; Tursch et al., 1972, 1975. ²⁷Dimethyl disulphide, Casnati et al., 1967; Crewe and Fletcher, 1974; Crewe and Ross, 1975. ²⁸n-Hexanal, Waterhouse and Gilby, 1964; Waterhouse et al., 1961. ²⁹2-Methylene-butanal, Wallbank and Waterhouse, 1970; Waterhouse and Wallbank, 1967. ³⁰Glomerin, Meinwald et al., 1966c; Schildknecht, 1971, 1970; Schildknecht et al., 1966. ³¹Phenylethanol, Aplin and Birch, 1974. ³²p-Hydroxybenzaldehyde, Miller et al., 1973; Schildknecht, 1971, 1970; Staddon and Weatherston, 1967. ³³Aristolochic acid I, vonEuw et al., 1968; Rothschild, 1972; Rothschild et al., 1972. ³⁴Marginalin, Schildknecht, 1971, 1970. ³⁵n-Pentanoic acid, Blum, 1974; Brand et al., 1973a. ³⁶2-Methylcyclopentanene, Wheeler et al., 1975. ³⁷Skatole, Blum et al., 1973b. ³⁸Methyl 8-hydroxy-quinoline-2-carboxylate, Schildknecht, 1971, 1970; Schildknecht and Tacheci, 1971. ³⁹2,3-Dimethyl-benzoquinone, Eisner et al., 1974a, 1971c; Fieser and Ardao, 1956. ⁴⁰Mellein, Brand et al., 1973a. ⁴¹Methyl 4-methyl-pyrrole-2-carboxylate, Riley et al., 1974; Tumlinson et al., 1971. ⁴²Methyl homogentisate, Schildknecht, 1971, 1970. ⁴³n-Propyl-naphtho-quinone, Tschinkel, 1975a. ⁴⁴Cantharidin, Carrel and Eisner, 1974; Cavill, 1969; Cavill and Clark, 1971; Meyer et al., 1968; Schlatter et al., 1968. ⁴⁵Nitropolyzonamine, Meinwald et al., 1975. ⁴⁶Methyl 6-methylasli-cylate, Duffield and Blum, 1975. ⁴⁷2-Methyl-6-n-undecyl- Δ^1 -2-piperidine, Brand et al., 1972. ⁴⁸3,4-Dimethoxy-acetophenone, Meinwald et al., 1974. ⁴⁹n-Undecane, Bergstrom and Lofqvist, 1970, 1968; Blum, 1974; Brand et al., 1973.

It is regrettable that biologists and chemists have not generally applied equally assiduous analyses to proofs of the role(s) of allomones in arthropod biology as have chemists in their proofs of chemical structures. This extreme argument of the division of scientific labor views the compendium of factual chemical data as most often being supported by bioassays that merely rely on the persuasion of limitedly researched hypotheses, rather than on the force of an extensively verified hypothesis (theory). Thus, the accusation was made that literature describing the role of allomones was too anecdotal. Evidence has been forthcoming for over a hundred years that arthropod exudates have the potential to deter some predators. This phenomenon is now a truism, and our familiarity with it has probably bred contempt. It is a scientific sinecure to offhandedly relegate allomones the function of parrying attackers on the bases of a few selected bioassays. The investigation of the supposedly commonplace phenomena of allomones being selectively advantageous for the liberators and antagonistic to the attackers is not a mundane scientific problem. A high degree of resolution at the genetic, biochemical, organismal and ecological levels is required before our thoughts on allomones will be sophisticated.

There is a reasonable body of data to demonstrate that defensive secretions are often repulsive to a large variety of vertebrate and invertebrate predators. Some of this data can be gleaned from the following references; Aplin et al. 1968, Benfield 1972, 1970, Blum 1961, 1969, Blum and Edgar 1971, Blum and Sannasi 1974, Blum et al. 1973a, 1973b, 1972, 1971, 1969, Boyden 1976, Brand et al. 1973a, 1973b, Brower 1970, Carrel and Eisner 1974, Chadha et al. 1962; Cloudsley-Thompson 1968, Cuénot 1896, 1890, Duffey et al. 1976b, Duffield et al. 1974, Edwards 1966, Eisner 1970, Eisner and Eisner 1965, Eisner and Meinwald 1965, Eisner et al. 1975, 1974a, 1974b, 1972, 1971a, 1971b, 1971c, 1970, 1961, vonEuw et al. 1971, 1968, 1967, Hepburn et al. 1973, Hurst et al. 1964, Kistner and Blum 1971, Kluge and Eisner 1971, Licht 1969, 1968, Lopez and Quesnel 1970, Marsh and Rothschild 1974, Maschwitz et al. 1972, 1970, Meinwald et al. 1975, 1968a, 1968b, 1968c, 1966, 1962, Miller and Mumma 1973, Miller et al. 1975, Moore 1968, 1967, 1964, Pasteels et al. 1973, Pavan and Dazzini 1971, Roth and Eisner 1962, Rothschild 1975, 1972a, 1972b, 1966, Rothschild and Aplin 1971, Rothschild and Kellet 1972, Rothschild et al. 1973, 1972, 1970b, Schildknecht 1971, 1970, Schildknecht and Tacheci 1972, Schildknecht et al. 1975, Tschinkel 1975a, 1975b, 1975c, Wallace and Blum 1969, Waterhouse and Wallbank 1967, Wheeler et al. 1972a, 1972b, 1970, Wood et al. 1975, Woodring and Blum 1963, Yang and Kare 1968.

However, from such data we have very little basis to formulate accurate concepts of the predator prey-interaction, or infact to deem our antipredator hypothesis adequately proven. The descriptions of the chemically mediated confrontation of prey and predator suffers for several reasons. One is that too much of our emphasis has been placed upon the allomone as the sole instrument of effrontery rather than upon the repulsed organism. It is the receptivity of the predator that predominantly determines the effectiveness of the allomone, not the chemical. Another is that too frequently the test of the deterrent potential of an allomone is based on laboratory criteria (*ex situ*), rather than on conclusive or corroborative tests in the field (*in situ*) where the advantages accruing from allomones (e.g., reproductive success) might be more realistically measured. Cynically, many of the reported examples of defensive effectiveness can be counted as false positives until it is established that the test organisms represent natural rather than experimentally benign and artificial predators. Essentially, one could similarly assay butanol, acetone, pyridine, benzene or a variety of other common laboratory chemicals for their deterrent potential. Owing to the irritable nature of living tissues, it would be expected with a high degree of frequency that these foreign chemicals would be repulsive to non-adapted organisms (intolerant). Surely one can not assume that allomones have evolved solely to ward off intolerant predators some of whom actually may not represent a significant force in the prey's life. The significance of allomones in relation to a spectrum of predators (intolerant, tolerant, insensitive) is unknown. Even a minimal defensive effectiveness against a tolerant predator may be advantageous in conjunction with other defensive mechanisms (see Feeny 1975 re herbivores versus plants). Estimations of the natural biological relevance of arthropod allomones are sorely needed.

Two allomonal systems that have achieved notoriety are the spiroboliform millipedes which secrete a mixture of benzoquinones (Barbier and Lederer 1957, Eisner and Meinwald 1966, Eisner 1970), and the polydesmoid millipedes which secrete hydrogen cyanide (HCN) and benzaldehyde (Wheeler 1890, Blum and Woodring 1962, Eisner 1970, Eisner et al. 1963a). The liberation of these

chemicals is not restricted to the above organisms. Phalangids (Eisner et al. 1971c, Fieser and Ardao 1956), beetles (Moore and Wallbank 1968, Tschinkel 1975a), cockroaches (Wallbank and Waterhouse 1970), true bugs (Roth 1961), termites (Maschwitz et al. 1972, Moore 1968, Wood et al. 1975), earwigs (Eisner 1960, Schildknecht and Weis 1960), and grasshoppers (Eisner et al. 1971a) secrete benzoquinones. The production of HCN coupled with benzaldehyde is observed in a more limited variety of arthropods, a centipede (Schildknecht et al. 1968), and beetles (Moore 1967). Zygaenid moths apparently produce HCN but benzaldehyde has not been identified as a by product of cyanogenesis (Jones 1972, Jones et al. 1962).

Both HCN and simple benzoquinones (e.g., toluquinone) are toxic and chemically reactive molecules, which fortuitously have obnoxious odours. These qualities contribute to their putatively superb defensive characteristics. The ability of quinones to deter the feeding of some phytophagous insects has been correlated with the redox potential of these chemicals (Norris 1976, 1970, 1969, Norris and Chu 1974, Norris et al. 1970) and their interference with energy transduction at olfactory receptor sites by interacting with sulphur amino acids of the receptor protein (Norris 1976). The quinoidal secretions of tropical millipedes have been reported to blind chickens (Burt 1947). The Jamaican millipede *Rhinocricus holomelanus* can propel jets of quinone containing secretion up to a meter. Contact of this secretion with delicate tissues like the cheeks or underarms causes a painful stinging sensation, and within half an hour all contaminated areas of skin are tanned. Also, small amounts of this secretion applied with a fine paint-brush to the tongue of Anolis lizards results immediately in prolonged mouth-wiping followed by death (Duffey, unpublished data). With respect to HCN, more information is available about its toxic properties (Conn 1974, Jones 1972, Montgomery 1969) in mammals, yet less information is available concerning possible bases for its effectiveness in conjunction with benzaldehyde as an immediate defense against predators.

One cannot doubt that such allomonal secretions utilized by a given arthropod population are able in some way to reduce the number of successful attacks made by a variety of predators. However, such effronteries are not an absolute means of defense. Cloudsley-Thompson (1968) describes both HCN and benzoquinone producing millipedes being eaten by starlings and toads. Tiemann (1967) outlines the voracious eating habits of phengodid beetle larvae that prey upon both of the above kinds of millipedes. Eisner (1970) photographically demonstrates the irrelevance of the defensive secretions of the cantharid beetle *Chauliognathus lecontei* (dihydromatricaria acid; Meinwald et al. 1968b) to a predacious reduviid bug; likewise, the "grin and bear it" persistence of a grasshopper mouse overriding the copious release of anisomorphal by the walking stick *Anisomorpha buprestoides* (Meinwald et al. 1962). Unfortunately, as convincing as these type of data may be, there is a lack of data to demonstrate that in nature these allomones provide the hypothesized advantage. In fact, there is little evidence to substantiate that the major function of such allomones is primarily for defending oneself against large predators. If we consider that millipedes and many beetles live within the top layers of the soil, it is reasonable to suppose that the depredations of bacteria, fungi, parasitic worms and a variety of other less visible predators are a significant force in their lives.

Our present bank of data presents too simplistic a view of allomonally mediated interactions between organisms. The rub of the science is that an hypothesis is not always amenable to testing. Although Brower (1970) was able to demonstrate convincingly in the laboratory that sequestered cardenolides in the Monarch butterfly were an adequate chemical basis for supporting Batesian-Mullerian mimicry, he and his colleagues had technical difficulties verifying that Batesian mimics (moths and butterflies) were at a selective advantage in a neo-tropical jungle (Brower et al. 1967b, Cook et al. 1967, but see Waldbauer and Sternburg 1974). It is only to our loss that more of these essential types of studies, often difficult and very laborious, are not more frequent. Similarly, biologists have not been able to conclusively demonstrate any definite functions for the phenomenon of cyanogenesis in plants, bacteria and fungi (Conn 1974, Eyjolfsson 1970, Hutchinson 1973, Jones 1972). The dilemma, therefore, is to corroborate the findings of *in vitro* studies with those of field studies.

The interaction between the prey and the predator involves not only the appropriate ecological circumstances, but also a complexity of behavioral, physiological and biochemical occurrences in both organisms. The allomone by definition is indexed by its effect upon the behavior and physiology of the predator during the attack. The following colloquial terms are extensively used to describe the allomone; chemical defense, repellent, and deterrent. It is unfortunate that these terms are used synonymously in reference to arthropod allomones, for in the context of plant allomones and kairomones they are used somewhat more rigorously (Beck 1965, Schoonhoven 1969, Thorsteinson

1960) to segregate various behavioral aspects of insect feeding. Nevertheless, in both contexts these terms are inadequate to accurately portray the inherently complex and varietous behavior of animals. Erecting additional neologies at this point in time will serve only to make our visions more opaque.

Some of these descriptive problems can to a degree arise from the nature of our language. In other words, the epithets, deterrent *et cetera*, are active rather than passive concepts; we are not merely concerned with the chemical deterrent (active voice) but we are also concerned, by definition, with the organism that is deterred (passive voice). Thus, the words deterrent *et cetera* unconsciously focus our attentions on the chemical mediator rather than on the receiver (the physiological and behavioural means by which the predator is excluded from meal). The allomone has no context unless its properties can be realized in relation to an irritable organism. One further point, which arises from the lack data on the complete chemical composition of allomonal secretions, is that the *natural context* of an allomone is only as a component of the mixture of chemicals that comprise the secretion. This is such an important facet of understanding the efficacy of defensive secretions, it is surprising that so few investigations have been undertaken to illuminate the defensive advantages arising from multicomponent secretions. In many cases, the chemical data is certainly available to show the multicomponent nature of defensive secretions; yet, the biological activity of the secretion is often depicted in terms of the major component (e.g., benzoquinones, HCN, glomerin). This is reminiscent of the state of affairs 5-10 years ago in the field of insect pheromones where the predominating thought was that there existed a specific chemical for a specific insect. As Silverstein and Young (1976) so aptly write, “what happened to lead so many investigators astray? Why was the “magic bullet” concept – one insect, one specific compound – so firmly planted”?

Chemical complexity and bases of defensive effectiveness

Ghent (1961) demonstrated that the mixture of formic acid and citronellal in formicine ant secretions was an adaptive defensive feature; the citronellal functioned as a solvent and thereby added in the penetration of the more noxious formic acid into the cuticle of the foe. Eisner et al. (1968) also described the essentiality of small amounts of caprylic acid in the aqueous formic acid secretion of the whipscorpion *Mastigoproctus giganteus*. The presence of caprylic acid enhances the action of the secretion by acting as a wetting and penetrating agent. Likewise, many lipophilic substances (esters, alkanes, alcohols, aldehydes, alcohols) which by themselves are reported to have limited allomonal properties, have been shown or postulated to lend more immediate and intensified deterrent properties to a defensive secretion contacting both vertebrate and invertebrate predators (Bergström and Löfqvist, 1970, Blum 1970, 1969; Eisner 1970, Gilby and Waterhouse 1965, Remold 1963). The means by which this intensification is accomplished are through the physico-chemical properties of the chemicals (e.g., solvency, surfactancy, volatility). It would be refreshing to read publications describing these phenomena based on more detailed physical, physiological or behavioral analyses, rather than on non-parametric crude bioassays.

It is claimed that many high molecular weight components of defensive secretions (e.g., *n*-tridecane, *n*-undecane) function to a large extent to reduce the rate of evaporation of lower molecular weight offensive components. I am unaware of any studies that prove this hypothesis by physical data. It would be interesting to know, for instance, whether the alkenals and alkenyl acetates in admixture with alkanes (scent gland of *Nezara viridula*; Gilby and Waterhouse 1967) represent an optimized physico-chemical system for defense by comparison with admixtures of non-biological homologues. Similar studies might be very fruitful with the alarm-pheromonal system of the ant *Lasius* (Bergström and Löfqvist 1970). This line of reasoning, although initiated years ago (Wilson and Bossert, 1963, Wilson 1970), has not even passed the germinal stages.

Along similar lines of thought, it would be more fruitful to view the multicomponent defensive secretion both in the native and dissected state. As an example, the HCN and benzaldehyde liberated by polydesmoid millipedes has been accredited as a highly offensive system against most predators (Blum and Woodring 1962, Eisner 1970, Eisner et al. 1963a, Eisner and Eisner 1965). In the natural context, this claim is now oversimplified, for it is not explicit in these statements (especially to the casual reader) that HCN and benzaldehyde may only be components, not sole agents, of a complex mixture. This may seem like a picayune point, but I feel that the science would prosper more by scientifically accurate statements rather than by pragmatic ones.

Polydesmus collaris collaris has been shown to produce isovaleric, formic, and acetic acids along with HCN and benzaldehyde (Casnati et al. 1963), a variety of cyanogenic polydesmoid millipedes have been shown to produce phenol and/or guaiacol (Blum et al. 1973a, Duffield et al. 1974, Duffey et al. 1976a, Monteiro 1961), and the secretions of many xystodesmid polydesmoids seem to be characterised by considerable inclusions of benzoic acid, benzoyl cyanide, and mandelonitrile benzoate (Duffey et al. 1976b). Phenol, guaiacol, and benzoyl cyanide are adequate defensive agents in themselves in artificial conditions, let alone in admixture with HCN and benzaldehyde; whereupon, the defensive effectiveness is enhanced. Studies would be invaluable describing, with physical data, how each of these components modifies the physical properties of the defensive secretion such that it is or is not effective against a given range of predators with somewhat specified dermal-epidermal or cuticular properties. Likewise, it would be invaluable to have some perceptive bioassays that could demonstrate, for example, additive or synergistic activities of given components (with reference to the whole) as a physiological or pharmacological investigation of the response of a predators. Scientists working on pheromones and plant-insect relationships seem to have accomplished some of these tasks, besides having a wealth of descriptive and chemical data.

The efficacy of an allomone need not necessarily rely upon its fetid, irritating or distasteful properties, although it would seem reasonable in most circumstances to attribute the immediate deterrent nature of chemicals like HCN-benzaldehyde, benzoquinones, isobutyric acid (Eisner and Meinwald 1965, Quesnel and Lopez 1970, Pattenden and Staddon 1972, Seligman and Doy 1973, 1972), and hemipteran scent components (Calam and Youdeowei 1968, Games and Staddon 1973a, Hepburn and Yonke 1971, Waterhouse et al. 1961) to their odorous properties (at least in vertebrates). Chemicals like the alkaloid prococcinelline II found in coccinellid beetles (Pasteels et al. 1973), and the isoquinazolinone alkaloid, glomerin, produced by the millipede *Glomeris marginata* (Meinwald et al. 1966c, Schildknecht et al. 1966) may rely on their bitterness as the initial line of defense.

Instead of these blatant perceivable (obvious) effronteries to the olfactory-gustatory perception or sensitive tissues of the predator, certain recent studies indicate that more subtle manipulation of the predator can arise by imperceivable (cryptic) distortions of its peripheral perception. This dichotomy of the obvious versus the cryptic can be exemplified by several human phenomena. Those fond of oriental cooking will be aware of the excellent taste of the food but will be unaware that inclusion of monosodium glutamate is accentuating their perception of certain tastes. Likewise, it would be anathema for a trained wine taster to inhale cigarette smoke prior to tasting a fine wine, since it would predispose his taste buds to an inaccurate assessment of the wine. This distortion of gustatory acuity is not a perceivable phenomenon, although, the taste of the smoke itself might be disagreeable. Certain of these subtle distortions will be discussed briefly below, for want of more articulate terms as anaesthetics, distorters or modifiers, intensifiers, jammers, maskers, and fixatives.

Recently, certain allomones have been implicated as anaesthetics. Pregnane based steroids have been identified in the defensive secretions of aquatic dytiscid beetles, and in extreme bioassay conditions shown to cause stupor or a response akin to anaesthesia in fish (Schildknecht 1971, 1970, Schildknecht et al. 1967a, 1967b). Likewise, norsesquiterpenes have been isolated from the secretions of gyrinid beetles (Meinwald et al. 1972, Miller et al. 1975, Schildknecht et al. 1972), and also in extreme bioassay conditions shown to anaesthetize minnows (Miller et al. 1975). Despite the artificial bioassay conditions employed to investigate both anaesthetic agents, these useful studies do point to the possibility of aquatic predators like fish experiencing stupor or lowered perceptual abilities by the ingestion of small numbers of these insects. Unfortunately the appropriate bioassays have not been carried out to test the feasibility of such hypotheses.

Apparently the non-specific mechanism for steroid anaesthesia is poorly understood, although deep steroid anaesthesia is accomplished by internally injected doses of steroids, or by rapid absorption through the gills from unnaturally high test concentrations. This also applies to the gyrinid norsesquiterpenes. However, the narcotic hypothesis is insufficient to explain the more immediate deterrent properties of norsesquiterpenes against fish (Benfield 1972, 1970). The deterrent nature of these chemicals may arise from their ability, at least for steroids, to effect the electrical output of fish olfactory organs (Oshima and Gorbman 1968). Both the dytiscid and gyrinid allomonal system present challenging ecological problems in which both immediate and delayed responses are induced in the predator. Clear definitions of the roles of these systems will require the integration of expertise from many scientific fields.

Another allomonal system that appears to narcotize arthropod predators is the HCN-benzaldehyde system of polydesmoid millipedes. A variety of polydesmoids have been shown to produce benzoyl cyanide as one of the many components of the cyanogenic secretion (Duffey et al. 1976b). Benzoyl cyanide is not only lacrimative to mammalian eyes, but also seems to cause "local anaesthesia" upon short-term contact of the vapor with the antennae of ants. Upon longer exposure to the vapours ants become ataxic and behave as if they were anaesthetized; after an hour or more, depending upon the time of exposure and the concentration of the gas, the ants recover. A variety of insect experience rapid "knock-down" after contact with vapours of benzoyl cyanide. The mechanism of this "anaesthesia" is not known, although it could be speculated that the amphiphilic properties of benzoyl cyanide are suited for immediate and prolonged dissolution in the antennal membranes (Duffey et al. 1976b). Benzoyl cyanide is an extremely reactive molecule; it has the potential to benzoylate OH, NH, and SH functions (Dornow and Theidel 1954), as well as being a potential acylating agent (^-CN). It is possible that benzoyl cyanide could exert part of its local anaesthetic effect (as well as long term toxic effects) by chemically reacting with OH, NH, SH functions, and thereby fixing the membrane. This would disrupt the quality of further antennal perception. Even if this is not the case, the irritant and odorous properties of benzoyl cyanide in admixture with HCN, benzaldehyde and other chemicals are probably highly functional as an immediate deterrent against some predators.

The chemical fixation of receptive membranes or even sensitive tissues by direct contact with allomonal secretions is feasible. *p*-Benzoquinones are other likely candidates for chemical fixatives; these chemicals also have the ability to react covalently with NH_2 , SH, and aromatic functions (Fieser and Ardao 1956, Hackman and Todd 1953, Kuć, 1972, Moxon and Slitkin 1972, Rich 1969). Thus, aside from irritating odour of benzoquinone containing secretions which can lead to immediate deterrence of a predator, closer contact with the liquid secretion, instead of its vapours, may result in a prolonged sensory handicap for the predator. The tanning properties of the Jamaican millipede *Rhinocricus holomelanus* have been previously mentioned. The work of Norris (1976) suggests that some benzoquinones may have more than momentary associations with the gustatory membranes of phytophagous insects. These prolonged chemical associations, based on redox potentials of quinones, in essence represent chemical fixation of the membrane.

The norsesquiterpene, benzoyl cyanide, or benzoquinone containing defensive secretions provide superb allomonal systems to obtain detailed physiological, biochemical, physical, and behavioral data on the reactions of predators.

Perception of allomones in relation to defense

The theories of taste and odour perception are too complex to outline in this discussion in any detail. One model of the nature of perception is as follows. A receptor organ such as an insect antenna exposes itself to a flux of a variety of molecules in the contiguous atmosphere. Only a limited number of species of molecules will have both an affinity for the receptive surface of the organ and an ability to induce changes in this surface. It is thought the special stimulant molecules first associate with the receptor membrane by physico-chemical processes. In other words the first association between the stimulant and the receptor protein relies on non-covalent absorption (solubility and/or intermolecular forces). It is during this initial ephemeral association that olfaction occurs; the stimulation of the receptive membrane is achieved by the stimulant molecule inducing conformational changes in the receptive site that place the membrane in an excited state. Supposedly at this point nerves interpret the excitation (Beets 1970, Jaenicke 1974, Kafka and Neuwirth 1975, Kafka et al. 1973, Preisner et al. 1975). Subsequent removal of the stimulant molecule from the receptive surface occurs by several means; short residual life on membrane surface (evaporation); enzymatic degradation; and covalent or stable non-covalent binding to non-enzymic proteins (Beets 1970, Ferkovich et al. 1973, Kasang 1974, 1971, Kasang and Weiss 1974). These latter steps are considered to represent detoxication processes such that inappropriate stimulation of the membrane does not occur by molecules with long residual lives.

However, some authors are postulating, as in the case of α -glycosidase sugar-receptors (Amakawa et al. 1975, Koizumi et al. 1974), that these moderately specific enzymes may be the receptor system. It has not been ruled out that these enzymes merely remove the stimulant molecule; but the concept is an appealing explanation for gustatory specificity in feeding. Nevertheless, it is reasonable to envisage from the above explanation that both specific and non-specific sensory

perception can occur. A receptor site subject to conformational change only under the influence of a limited spectrum of molecules (bombykol, Kasang, 1974, 1971, ATP, UDP, ADP, Smith and Friend 1972) can represent a specific system. On the other hand, a variety of receptor sites or the whole membrane surface may be subject to non-specifically induced physico-chemical changes from a variety of chemical species. Many molecules possess the ability to alter the surface tension of membranes; this results in a change of the testing potential of the membrane (altered ion flux) (Tanford 1973). This also could give rise to non-specific perception with the appropriate nervous translation.

How can the phenomenon we describe as deterrence, repellency, *et cetera* be dissected in terms of this model? Risking speculation, one can view allomones as interfering possibly both specifically and non-specifically with receptors or associated membranes.

The perception of favorable and unfavorable molecules, whether they be pheromones or substances encountered during feeding, can be correlated with electrical changes (electroantennograms or single cell recordings) in the olfactory organs (Dethier 1974, Floyd et al. 1976, Jaenicke 1974, Payne 1975, Schoonhoven 1972, 1969, Washio and Nishino 1976). These electrical changes are either the result of specific molecules impinging upon highly selective receptor sites (frontalin, brevicomin, and terpene hydrocarbons in *Dendroctonus* spp.; Payne 1975), or the result of a variety of molecular species with similar 3-dimensional molecular shapes and/or common functional groups impinging upon (a) receptor(s) with broader specificity (Dethier 1974, Floyd et al. 1976, Kasang 1974, Washio and Nishino 1976). Depending upon the neurophysiological makeup of the animal, these alterations of the electrical state of the receptor cell will induce a variety of behaviors (attraction, repulsion, feeding, mating *et cetera*). On the other hand, some chemicals may be neurophysiologically irrelevant because they lack the ability to alter a receptive system (Floyd et al. 1976). Olfaction and gustation based on these mechanisms should then be highly susceptible to manipulation by chemicals foreign to that organism. Probably, most organisms have an array of receptors designed to perceive a spectrum of chemicals.

Allomonal and pheromonal arthropod secretions are often complex mixtures of chemicals, not all components of which have intrinsic allomonal or pheromonal activities (Blum 1974, 1969, Blum and Brand 1972). Many of these "non-active" components have been assigned the functions of organic carriers, surfactants, penetrators, and evaporatory retardants. In particular, aliphatic compounds (alkanes, -ols, -als, -enols; e.g., undecane, dodecanol) admirably suit the prescription because of their physical characteristics. The presence of such compounds in arthropod secretions is very widespread (Bergström and Löfqvist, 1968, Blum 1974, Blum et al. 1973b, Brand and Blum 1972, Brand et al. 1973a, Cavill and Houghton 1974, Eisner et al. 1974, Eisner 1970, Happ 1968, Hurst et al. 1964, Regnier and Wilson 1969, 1968, Tschinkel 1975a, Weatherston and Percy 1971). Because of their wide spread occurrence and associability with biological tissues, it has been proposed that such chemicals may function as antipredator devices by "jamming" receptor sites of chemoreceptors (Blum 1974, Blum and Brand 1972). The essence of this hypothesis is that one or several compounds in the defensive secretion interact with the chemoreceptor(s) of the predator causing an alteration of the normal receptive state. This alteration results in loss of perceptive acuity or possibly temporarily "blinds" the predator by preventing the recognition vital chemical cues. This argument also stresses that a complex mixture of alkanes may be highly advantageous because of the potential to cause a dysfunction in several types of chemoreceptors besides synergistically or additively increasing the overall effect of the secretion. This is akin to the concept of "negative odours" wherein certain chemicals may have the ability to alter the dendritic membrane potential (Kittredge et al. 1974), which in turn reduces the perceptiveness of the predator. Likewise, in certain environmental circumstances complex allomonal mixtures may be advantageous in coping with a spectrum of physically, physiologically and behaviorally different predators.

If one endorses the physico-chemical model of chemoreception where olfaction occurs at the time of absorption on the receptive surfaces, one can to a limited degree envisage how "jamming" could occur. Many allomones are lipophilic or amphiphilic and should dissolve readily either as a gas or liquid (Fries 1973, Hutchinson 1973) in membranes; propinquity of the predator during the defensive release of the allomonal fluid will certainly aid in topical or bodily application of liquid and/or concentrated vapour. At this point, large scale dissolution of the allomone(s) could occur in the membranes of the receptive organism. Surely this would not predispose the membrane and receptive areas to natural functioning, particularly if a defensive component had surface active properties. As previously mentioned, chemicals that interfere with the surface tension of membranes

can lead to altered ion fluxes (Ehrenpreis et al. 1969, Tanford 1973). Even if such chemicals have no surfactant properties they may be able to dissolve in membranes and derange critical membrane configurations. The toxicity of certain solanaceous alkaloids, e.g., tomatidine, and the macrolide antibiotic filipin are discussed in relationship to disturbance of membrane integrity (Kinsky 1970). Thus without even reacting with receptor sites perception could be distorted by creating inappropriate stimuli or causing a lack of appropriate electrical stimuli for the nerve cells. On the other hand the components of a defensive secretion may merely "flood" the sense organs of a predator making the perception of pertinent chemical cues difficult, or non-specifically putting the predator in perceptive imbalance.

It would be interesting to compare the solubility and residual life of individual and admixed natural defensive products with those of abiological products. Perhaps one would observe that some or many allomones, despite their volatility, have a greater propensity for certain biological tissues, and once they are in solution or absorbed have greater residual lives. The previous arguments for penetrant and surfactant functions are not in discord with this question. The residual life or rate of evaporation of the contaminant from the tissue will certainly be a factor in determining the amount of damage, irritation, or dysfunction induced in the predator. The residual life will partially be dependent upon the solvent characteristics of other components in the defensive secretion. The residual life of ^3H -bombykol on the antennae of *Bombyx mori* was influenced by the type of solvent used in the application of the pheromone (Kasang 1974). Perhaps, some allomonal secretions in the appropriate biological context, are subtle blends that maximize in many ways the potential to interfere with the physico-chemical and physiological organization of a foe? The residual life of skatole is hypothesized to be a factor in the defence of lacewings against bats (Blum et al. 1973b), dissolution in the predator's tissues provides a lingering reminder of the prey.

There are many other possibilities for allomonal distortion of gustatory and olfactory senses (Rohan 1972). The salts of chlorogenic acid and cynarin modify the human perception of water so that it tastes sweet (Bartoshuk et al. 1972). On the opposite scale, gymnemic acids (saponins) suppress the taste of sweetness in man; these chemicals did not appear to effect insects in the same way (Eisner and Halpern 1971). Undisclosed organic molecules are also able to modify the nose so that malodorants are imperceivable (Maugh 1975). Yet, it is not unreasonable to consider that arthropod allomones can in some instances function as jammers, modifiers, distorters, or what have you, rather than to only consider deterrence *via* irritant or fetid properties.

Certain examples from the pheromonal literature may be relevant if extrapolation is realistic. Some allomones might positively synergize the response to predator to a specific odorant present in the defensive secretion. Many examples of intensification or synergism by natural and synthetic chemicals are cited in the pheromonal literature (Birch 1974, Blum 1974, Blum and Brand 1972, Cardé et al. 1975a, 1975b, Shorey 1973). Brady et al. (1971) demonstrated that males of the indian meal worm were attracted to a pheromone liberated by the female only when an additional compound emanating from the female sex gland was present. The European elm bark beetle *Scolytus multistriatus* has a mixture of 3 main pheromonal components (-)-4-methyl-3-heptenol, multilure, and multistriatin released by virgin females. Individually these chemicals are unattractive to males but in admixture they are highly attractive (Pearce et al. 1975).

Alternatively, one can argue for some allomones negatively synergizing or inhibiting the perception of specific odours by specific predators. Many insect pheromonal systems are susceptible to inhibition by natural and synthetic chemicals (Arn et al. 1974, Birch and Wood 1975, Blum and Brand 1972, Kullenberg and Bergström, 1975, Kullenberg et al. 1971, Roelofs and Comeau 1972). The gypsy moth female can produce an olefin from its sex gland which inhibits the attractiveness of disparlure to males (Cardé et al. 1973). It has also been observed that dodecyl alcohol can synergize the perception of disparlure; while the corresponding acetate inhibits perception (Roelofs and Cardé 1974). Of interest is the observation that hexanoyl chloride causes violent combat amongst ants (*Conomyrma pyramica*, Metcalf and Metcalf 1970); it was suggested that this chemical obliterated the ability of the ants to perceive their natural alarm pheromone 2-heptanone. Such examples might make the investigation of the poorly understood synergism, masking (jamming) *et cetera* in allomonal situations very fruitful, whether these effects be mediated by peripheral and/or central nervous phenomena.

At present our understanding of the immediate aspects of deterrence in a predator-prey interaction is very limited not only as a physio-biochemical phenomenon, but also as a behavioral and ecological one. A difficult problem in many instances is to devise a bioassay that is biologically relevant. Field corroborations are difficult. They are so few and perhaps a dead art because of the magnetism of laboratory science. Very few modern reports of analyses of arthropod allomones and/or their effects upon various predators are relatable to modern field observations of predation. Instead, they (Blum et al. 1973b, Carrel and Eisner 1974, Benfield 1972) must rely on historical anecdotes of predation and defense. Obviously, one scientist interested in chemical analyses can not be held to task for avoiding meaningful predation studies, nor should the physiologists or biochemist bear the onus. There seems to be a lack of the field-scientist who will shrewdly couple his mind with the above scientists and prove a hypothesis with a wealth of interdisciplinary data derived from field and laboratory experiments.

Unfortunately the laboratory bioassay of the efficacy of an allomonal secretion against predators has become an embellishment of the investigative process. Despite what may arbitrarily be termed feats of structural chemical analysis (MacConnell et al. 1971, Meinwald et al. 1975, Pasteels et al. 1973, Schildknecht 1970, Smalanoff et al. 1975, Wheeler et al. 1975) or of morphological analysis (Eisner et al. 1964, Eisner et al. 1963a, Happ 1968, Kendall 1974, Tschinkel 1975c, Woodring and Blum 1963), the bioassay has not been wielded as a highly incisive technique. In many instances it is difficult to devise a biologically relevant bioassay, one that is an accurate approximation of the *in situ* interaction of the allomone(s) with the predator(s), and in particular one that is not a reiteration of what can be observed casually in the field. For instance, ants are often one of the arbitrary laboratory predators, chosen because of their obvious abundance and proximity to the niche of the prey. By artificially placing a prey like cyanogenic millipedes (Blum et al. 1973a, Duffey et al. 1976, Eisner 1970), alkaloid bearing beetles (Pasteels et al. 1973), or quinone producing arthropods (Eisner 1970) in contact with such predators one most often obtains the desired deterrent effect.

An interesting turn of affairs is observed in several genera of neotropical myrmecophilous millipedes associated with army ants. Rettenmeyer (1962) reported that he could find no evidence of defensive glandular secretions (e.g., *Calymmodesmus gracilis* or *Rettenmeyeria parvipes*) or of the ants (e.g., *Labidus praedator* or *Nomamyrmex esebecki*) being deterred by any of the millipede genera studied. "I have repeatedly seen other non-myrmecophilous millipedes walk through swarm raids and raid columns of Neotropical army ants, *Eciton* and *Labidus*. In most cases the ants did not attack the millipedes but occasionally a few ants would bite a milliped's legs. The ants always released the milliped, but it was unclear whether any defensive chemical was released. We have examined hundreds of prey samples collected from army ant colonies and have no evidence that millipeds are ever captured by these ants" (Rettenmeyer, personal communication). Are the myrmecophilous millipedes adapted to release pheromones which placate the ants as has been observed in myrmecophilous beetles (Kistner and Blum 1971, Hölldobler 1971)? Is the absence of millipede remains in prey samples from colonies an indication of a superbly effective chemical, physical, or behavioral defense? More field data of the above kind are needed.

Descriptions of meloid beetles liberating offensive chemicals upon prey by reflex bleeding has been known at least since 1890 (Cuénot 1896, 1890), the haemolymph harbours cantharidin (Meyer et al. 1968, Sierra et al. 1976), which is not offensive to all predators (Cuénot 1896, 1890, Selander 1960). Carrel and Eisner (1974) recapitulate some of the earlier findings, and quantify the feeding deterrent quality of cantharidin. They also establish that cantharidin can be perceived by a predacious beetle at concentrations down to approximately 10^{-5} Molar. Likewise, Duffey et al. (1976b) were able to establish that several species of ants in the laboratory were able to perceive benzoyl cyanide, phenol, and guaiacol at vapour concentrations of about 10^{-8} Molar. The relevancy of the inhibition of proboscis extension of a fly by polyzonimine from a millipede (Smalanoff et al. 1975) is obscure. None of these findings are in themselves surprising. In fact, they are rather predictable if one considers the taste and smell thresholds (Laffort 1963) for many natural products. Such assays are essentially not any more resolving than the statements of Cuénot. They merely document that in some instances the allomone is or is not effective as an *immediate* antipredation device.

We need to know *in situ* what type of predators interact with the prey (how, why, and when?), and what behavioural, physiological, physical, and biochemical traits predispose a predator to be successful or unsuccessful. These observations should be based on statistically valid data (if possible)

rather than on instances. With this range of studies we can begin to be articulate about the prey-predator interaction rather than just about the nature of the allomone. Boyden (1976) has attempted an interesting *in situ* approach to testing the palatability of butterflies to Ameiva lizards. By hanging various heliconiid butterflies over cliffs on fishing pole lines, he has hypothesized that the lizards establish their eventual responses to mimetic butterflies by gustatory cues. This study can surpass conjecture with the clever input of other disciplines. This type of test at least approximates natural conditions.

Delayed effects of allomones on predators

The immediate deterrent value of a defensive secretion is only one limited apparent facet of prey-predator interactions. Moreover, there is no sound evidence to suggest that the forces directing the evolution of allomonal defences were in the majority predators that would be immediately deterred. The often dramatic and visually convincing laboratory demonstrations of deterrence can reduce the scope of further curiosity (is this how defense works all the time?). To observe that a laboratory predator is deterred by a secretion gives no basis to extrapolate this phenomenon to the field. Hunger thresholds, or availability of natural prey may transform the formerly offensive organism into a tolerable food item. On the other hand, to find that a laboratory prey is acceptable to a predator is by no means to assess the long range aspects of that organism as a natural food item, especially if the predator naturally has many food choices. Also, the \pm results of short term predation studies may acquire different signs when analyzed in the field in terms of delayed effects upon the predator or changing physiological states of the predator. The long range effects of arthropod allomones are severely neglected phenomena, and may be found to be more important than previously considered.

Predation experiments with aquatic snakes, using minnows and worms as artificial mimics and models, have demonstrated that the snakes, through delayed ill-effects of lithium chloride injections after eating worms, learned to reject palatable minnows which have been artificially made to have an olfactory resemblance to the worms (Czaplicki et al. 1975). Brower (1969) has shown that the delayed pharmacological effect (emesis) of cardenolides upon jays is able to support a laboratory mimicry complex amongst butterflies. Many other defensive systems show dramatic and obvious delayed effects; the vesicatory action of cantharidin produced by meloid beetles (see Eisner 1970); and the narcotic effect of corticosteroids (Schildknecht 1970, Schildknecht et al. 1967b) and norsequiterpenes (Miller et al. 1975) produced by aquatic water beetles. More insidious delayed effects might be experienced by predators frequently eating tiger moths that contain poisonous senecio alkaloids (Aplin et al. 1969, Mattocks 1972), butterflies that contain aristolochic acids (von Euw et al. 1968, Rothschild et al. 1972), or even a variety of insects and myriapods that produce benzoquinones, phenolics, or HCN.

If one can extrapolate from mammalian toxicology to encompass a variety of other predators, it is not unrealistic to suppose that many allomonal systems have the potential to induce, within hours or days, severe or highly discomforting physiological stress in some predators. With the appropriate visual cues it may take a predator only a day or less to learn to avoid the prey. Surely, some allomonal systems require even longer time scales before the physiological side effects are intense enough to cause a formerly tolerant predator to begin to discriminate against that prey? Would it not be possible, after several days or weeks of feeding upon a given prey, for allomones to disrupt normal microorganismal populations or even essential symbionts (quinones, phenolics, aliphatic acids, terpenes), damage gut tissue by tanning (quinones, phenolics), or even to interfere with gut mobility or absorptive capacities (cardenolides, cholinergic agents) to the point where keenness or vigor of the predator would be reduced? Anthropomorphically, one could imagine some predators suffering from indigestion, afflatus, diarrhea, alimentary cramps and a variety of other malaises induced by defensive chemicals.

The growth rates of juvenile predators could be reduced by the ingestion of certain chemicals. Rehr et al. (1973a) have shown that L-DOPA is not only a feeding deterrent to phytophagous insects at high concentrations, but at lower concentrations actually reduces growth and increases mortality in the herbivore. Reese and Beck (1976a, 1976b) and Todd et al. (1971) have shown, for example, that *p*-benzoquinone, hydroquinone, duroquinone, L-DOPA, dopamine, protocatechuic acid, and catechol have detrimental long range effects upon growth, and morphogenesis of two phytophagous insects. Many of these above chemicals are present in insects as defensive agents or as products for cuticle

formation. Indeed, the potential toxicity of arthropod allomones to a variety of invertebrate and vertebrate predators is poorly known. One always finds tantalizing satellites of information such as hydroquinone being an antimetabolic agent (Dustin 1963, Goldstein 1969), or *p*-benzoquinones inhibiting fly ovarian development (Mitlin and Morody 1958).

Spurious information can also be found about other allomonal systems. Only a few examples will be given. Polyacetylenes such as dihydromatricaria acid isolated from the beetle *Chauliognathus lecontei* (Meinwald et al. 1968b) are well known components of many plants, especially composites and umbellifers (Bohlmann et al. 1968). Some polyacetylenes (e.g., *cis*- and *trans*-dihydromatricaria ester) are effective as antifungal agents (Drake and Lam 1974, Mitscher 1975). Their convulsant properties (Quilliam and Stables 1969) may be effective against herbivores and carnivores. Some polyacetylenes can also cause photosensitization. Many human populations suffer from the long term toxic effects of cyanide derived from food items like bamboo shoots and leguminous crops (Montgomery 1969). Certain saturated and unsaturated aliphatic acids are toxic and/or teratogenic to some insects (Quraishi 1972a, 1972b). Do any insects contain any proteinaceous material like phytohaemoglutinins (Janzen 1975, Liener 1974) or protein inhibitory factors (Liener and Kakade 1969)? It has been reported that protease inhibitors of plants interfere with the digestion of phytophagous larvae (Birk and Applebaum 1960, Green and Ryan 1972, Liener and Kakade 1969). Can any of these above phenomena be evidenced as natural defensive mechanisms of arthropods against predators?

Even more subtle means of manipulating the predatory population might be possible. One wonders whether the steroids present in incredibly high concentrations in aquatic water beetles (Miller and Mumma 1973, Schildknecht 1970, Schildknecht and Tacheci 1971, Schildknecht et al. 1967a) could have a more profound effect than narcosis upon predators like fish and amphibians. The powerful hormonal effects of steroids like testosterone, and cortisone upon vertebrates, especially mammals, is well known. Perhaps, by ingestion of prey or by proximity to prey, the extrinsically derived concentrations of these steroids over time are sufficient to interfere with reproduction or morphogenesis. Several steroids, like cortisone, are chromosomal poisons (Dustin 1963). Subtle manipulation by extrinsic hormones might be a very effective means of reducing or altering the structure of a predatory population. The liberation of dendrolasin from the mandibular glands of *Formica fusca* is apparently partly responsible for a proportion of apterae in ant-attended *Aphis fabae* (Kleinjan and Mittler 1975). The cyclic fluctuations of vole populations has been hypothesized to be a result of these mammals feeding differentially in time upon physiologically favorable and unfavorable plants (Freeland 1974). The favorable plants are consumed first; this alters the population structure of the plant community until the voles are obliged to eat physiologically damaging plants. A population decrease ensues. Could any similar phenomenon be occurring with predators feeding upon insects?

The design of a bioassay to determine the long range effects of allomones upon predators is a critical factor in determining the applicability of the bioassay to a meaningful understanding of the antagonism. Several studies have been carried out wherein allomones have been injected into the body of predators (Moussatché et al. 1969, Schildknecht and Tacheci 1971, Schildknecht et al. 1976a). The enteric discharges of grasshoppers are reported to be a topical irritant to eyes, cause vomiting after ingestion, and even result in death after the injection into the body (Eisner 1970, Freeman 1968). Similarly, Marsh and Rothschild (1974) have injected saline extracts of a number of toxic insects into the peritoneum of mice and observed the destructive effects of these injections upon internal organs. Although these bioassays in themselves are interesting, the relevance of wholesale injection of unpurified extracts containing a multitude of contaminants is questionable. The introduction of foreign proteins into the body cavity, which would otherwise not pass the gut barrier, can surely only result in severe anaphylactic shock. It is advisable to attempt to design bioassays that can demonstrate phenomena of allomones naturally impinging upon physiological systems.

Some interesting experiments by Hepburn et al. (1973) tested repellency of 27 different arthropod defensive chemicals against an omnivorous fish. Benzoic acid was deemed to be one of the most effective deterrents against the fish upon initial exposure. However, on further exposure to higher concentrations of benzoic acid it was found that the fish became tolerant to benzoic acid and accepted baits that would have been unpalatable to a naive prey. Habituation of predators to allomones could have severe effects upon a population of arthropods prey. One wonders if perhaps chemical complexity of defensive secretions might reduce the chances of predatory habituation. In fact, as Hepburn et al. (1973) point out, the structure of mimicry complexes may be subject to

dilution by a prominent organism which has an allomonal system of low deterrent character or one to which a predator can easily adjust. Thus, in a natural context, the long range effectiveness of an allomonal secretion may be extremely dependent upon the chemical diversity, and chemical complexity presented by a spectrum of prey to a spectrum of predators.

Predatorial breakthroughs

There will always be the predators who “walk on coals”, “sleep on nails” or have the legendary appetite of the goat. How does the predator become impervious to what is immediately repulsive or eventually non-desirable to other predators? Our knowledge of how such breakthroughs are made is extremely limited. How can toads and beetles eat with apparent impunity cantharid laden meloid beetles (Carrel and Eisner 1974, Cuénot 1896, Eisner 1970); starlings and toads eat cyanogenic and benzoquinone containing diplopods (Cloudsley-Thompson 1968); and phengodid beetle larvae voraciously eat both above kinds of diplopods irrespective of being bathed in the defensive secretion (Duffey et al. 1976b, Tiemann 1967)?

In some instances behavioral adaptations greatly enhance the acquisition of supposedly repulsive prey. The opossum mouse *Marmosa demararae* triumphs over the stick insect *Anisomorpha buprestoides* by initially tolerating a mouthful of anisomorphal, and then holding the insect in its paw until all the defensive fluid has been expended (Eisner 1965). Phengodid beetle larvae of the genus *Zarhipis* “go for the throat” of various spiroboliform and polydesmoid millipedes (Tiemann 1967). The larvae will actually wrestle with a much larger millipede for 5-20 minutes until the millipede tires, or the phengodid manages to insert its mouthparts through the gular plate. At this point the millipede is apparently paralyzed by some unknown substance. The beetle larvae throughout the struggle seem undisturbed by the copious release of benzoquinoid secretions. Besides the behavioral mechanism for capturing the prey, these phengodid larvae probably have evolved a cuticular surface that prevents spreading and penetration of the secretion over and into the body. One might also expect some biochemical adaptations which would enable the larvae to detoxify any internal insurgence of benzoquinones or other toxic agents present in the millipedes secretions. It is to be remembered that these beetle larvae are also voracious predators of cyanogenic polydesmoid millipedes (Tiemann 1967), so, in all, these larvae appear to have overcome two generally very potent lines of defense.

The ingestion of fair numbers of cyanogenic and quinone containing millipedes by toads and starlings (Cloudsley-Thompson 1968) also raises the question of how these predators overcome toxicosis. A number of possibilities exist. It may be that the predators handle the prey considerably before ingestion causing the prey to exhaust its defensive stores. However, it may be that the biochemical capabilities of the alimentary tract and/or the body in general are highly adapted for detoxication of a great variety of natural toxic products. Another possibility is that these predators could have a diverse population of alimentary microorganisms which carry out most essential metabolic transformations. Freeland and Janzen (1974) discuss this method of detoxication as a means for herbivores, especially, ruminants, to handle a variety of potentially harmful substances acquired from a diversity of plants. On the other hand, one must accept the possibility that an allomonal secretion may be totally irrelevant to some predators because of their physical, biochemical and physiological organization. Perhaps, these allomonal defenses are not as dynamic as we are led to believe?

It is an extreme view to consider that all defensive secretions are toxic. As previously discussed, the basis of effective defense may merely rely on the chance that the predator will perceive the allomone(s) as repulsive odors or tastes. Yet no life form is spared adversity. Such is the case for ants of the genus *Camponotus* that vie with the myrmicine ant *Myrmecia gulosa*. The former species produce copious quantities of formic acid as an alarm-defense system; the last species produce no formic acid, and is an effective predator of the formicine ants. During the attack the formic acid serves only to worsen the cause for *Camponotus* since the acid recruits more workers of *M. gulosa* and also intensifies the degree of onslaught upon the prey (Haskins et al. 1972). Inasmuch as one's defensive odor can be a salvation or a damnation, one's odor might also be totally irrelevant strictly because the given predator lacks the receptive systems.

Studies on the perception of various odorants by humans (Amoore and Forrester 1976, Amoore et al. 1975) show that not all individuals perceive chemicals identically, and that certain individuals are unable (anosmic) to perceive specific odors. These authors demonstrated that 7% of the human subjects were unable to perceive the odor of trimethylamine and 20% of the subjects were

anosmic to the odor of 1-pyrroline; anosmia to odors like isovaleric acid is also known. If one follows the argument that there should be no inherent fundamental difference between the mechanism of olfaction (and gustation) in insects and vertebrates, than it might be opportune to consider that such significant levels of anosmia might arise in an insect or vertebrate predatory population. If this were the case it might not be difficult for an anosmic predator to reap great benefits during its life cycle, or for the predatory population to evolve a fortunate relationship.

Understanding how predators overcome allomonal systems is the other hand of understanding how predators are repelled by allomonal systems. Perhaps, we lack a wealth of this type of data simply because the word allomone, untrue to definition, is synonymized with a chemical structure or an expedient bioassay, rather than viewed as a descriptive term for a thesaurus of susceptibilities in a spectrum of predators responding to a variety foreign of substances. The available literature clearly illustrates that many allomonal systems are amenable to field and laboratory dissection. Hopefully in future years more minds will be diverted to studying the designs of predators, as well as the designs of prey.

Cardenolides: defense and mimicry

I wish to consider one additional example of an allomonal system aimed at large predators; hopefully this example will demonstrate the need for an incisive interdisciplinary approach to a complex ecological problem.

The milkweeds serve as host plants for a number of larval and adult insects (Brower 1970, vonEuw et al. 1967, Reichstein et al. 1968, Rothschild et al. 1970a, 1973, Scudder and Duffey 1972). This association has provided some of these insects with the opportunity to evolve a chemical defense system based upon cardiac glycosides (cardenolides) sequestered from the host plant(s). The utilization of plant toxins as a method of defense in insects has also provided the means for many Batesian-Mullerian mimicry complexes to evolve (Brower and Brower 1964, Ehrlich and Raven 1964).

In particular, the Monarch butterfly *Danaus plexippus* has been shown to be involved in a geographically extensive Batesian-Mullerian mimicry complex (Brower 1958a, 1958b, 1958c). These mimicry complexes in part seem to be supported by the unpalatable nature of the tropical monarch butterfly (Brower 1969, Brower et al. 1968, 1967a), which results from the larval butterfly transposing sequestered cardenolides to the adult insect. The ability of certain cardenolides to induce emesis in vertebrates (Chai et al. 1973, Gaitonde and Joglekar 1972, Parsons and Summers 1971) has been used a laboratory means of bioassaying the palatability of adult Monarchs (Brower et al. 1968, 1967) to avian predators (jays) as well as other cardenolide containing insects (vonEuw et al. 1967, Parsons 1965). The ability of this butterfly to cause emesis in laboratory jays has been used as a criterion for concluding that these emetic insects are able to act as models in natural mimicry complexes. Swynnerton (1915) had also observed that captive birds vomited after eating African *Danaus* species. These experiments by the Browsers and cohorts constituted the first definitive proofs that insects were able, as Slater (1877) suggested, to sequester plant toxins and deploy them as highly effective chemical antagonists of large predators. Further analyses of this plant-butterfly relationship have reached the point where it is realized that the emetic potential of the adult is dependent upon the species of milkweed upon which the larvae fed. This is assumably the result of different plant chemistries (Brower 1970, Brower et al. 1975, Brower and Moffitt 1974, Brower and Glazier 1974, Brower et al. 1972). This phenomenon of differential emetic potential respective of larval feeding history has been termed the "palatability spectrum". Of all the arthropod allomonal systems, the cardenolide based one has received the most intensive and varied anecdotal, ecological, pharmacological, and chemical analysis (above Brower references, vonEuw et al. 1971, 1967, Parson 1965, Reichstein 1967, Rothschild 1973, 1972a, 1972b, 1966, Rothschild and Kellet 1972, Rothschild et al. 1975, 1975, 1970a, Scudder and Duffey 1972). Yet despite this moderate volume of literature, the understanding of the role of cardenolides as a chemical defense in insects is poorly understood and at a very general hypothetical stage.

I will initially argue from the standpoint that the basis of mimicry reinforced by sequestered cardenolides relies solely on inducing emesis in the predator (Brower 1969, 1970, Brower et al. 1968, Brower et al. 1973). It has been effectively demonstrated that several insects that feed upon asclepiadaceous plants contain enough cardenolides to cause emesis in experimental predators (Parsons 1965, vonEuw et al. 1967, Reichstein et al. 1968, Rothschild et al. 1973, Brower and Glazier 1974). Examination of the oral quantities of cardenolides required to induce emesis (Hoch

1961, Parsons and Summers 1972), reveals that about 0.1 – 1 mg/kg of predator is a functional range. Different species of animals can vary several hundred fold in their responses to cardenolides (Chen 1963, Detweiler 1967). Since one would not expect to find too many predators of cardenolide containing insects to weight a kilogram or more, any insect that can harbor 100 to 1000 micrograms of cardenolides has a reasonably high probability of being emetic. Insects such as lygaeid bugs (Duffey and Scudder 1974, vonEuw et al. 1971), the grasshopper *Poekilocerus bufonis* (vonEuw et al. 1967, Reichstein 1967), and some species of *Danaus* (Brower and Moffit 1974, Brower et al. 1975, 1972, Parsons 1965, Rothschild et al. 1975) are known to contain levels of cardenolides within this emetic range.

Yet, the possession of high levels of cardiac glycosides in the body of an insect does not necessarily mean that upon ingestion the predator will vomit. The lygaeid, *Oncopeltus fasciatus* in laboratory conditions contains 100-150 micrograms of cardenolide per insect (Duffey and Scudder 1974), yet when this insect is fed to captive artificial predators (toads, frogs, turtles, lizards, rats, praying mantis, chickens, and starlings) no deterrent or emetic effect is observed. Only the metathoracic scent glands were found to have any effective antipredator characteristics (Duffey and Scudder, unpublished data). It has also been observed that Monarch butterflies which have been fed upon *Asclepias syriaca* generally contain high levels of cardenolides in natural populations (Brower 1969, Brower et al. 1972) and are most often non-emetic to jays (Brower 1969, Brower et al. 1968, Brower and Moffit 1974). Rothschild and Kellet (1972) also observed that quail did not vomit upon ingesting potentially emetic Monarchs; whereas jays were found to vomit. How then can one begin to understand why in certain instances cardenolide containing insects are emetic and in others not?

Perhaps, the initial assumption that emesis, as a sole criterion for assaying the palatability spectrum, is an inadequate index of the impact of these chemicals in a natural predator population. Implicit in this querie are a number of other factors which must be considered in attempting to fully describe this particular plant-prey-predator interaction. One cannot assume that all cardenolides sequestered from the plant provide the same emetic potential, nor can one assume that all predators will exhibit equal sensitivity to a given dose. Inasmuch as the quail may represent an imperterbable artificial predator, so may the jay equally represent an artificially benign organism for bioassaying the physiological effects of cardenolides. Hence, both these extremes viewed independently, bias our interpretive powers! Also, to precis the qualitative and quantitative aspects of plant chemistry, the physiological and physical aspects of cardenolide sequestration in insects, and the multitude of factors determining the physiological response of a predator, as a simple function of emetic potential can only lead to naive concepts of the palatability spectrum. Another important question arises concerning the initial assumption; can a mimicry complex be supported in nature by the induction of other physiological stresses other than emesis in predators? I will briefly consider some of these questions.

The inherent intravenous (i.v.) emetic potential of a given cardenolide on a given predator may bear little relation to the emetic response induced by ingestion of that cardenolide. The reason for this is that several physiological systems of a predator can interfere with the theoretical dose-relationship response on the basis of ease of translocation of a cardenolide to the CNS emetic receptor. The first complicating factor in cardenolide translocation is the ability of that chemical to pass through the gut of the predator and enter the blood stream. The second major complicating factor, is the availability of that cardenolide to the emetic center once it is in the blood. Both these critical factors are regulated by the properties of gut and blood tissues. The gut can be highly lipidic and restrict the movement of certain cardenolides into the blood stream.

The blood stream can be highly selective in the type of cardenolides it binds to blood proteins a selectivity which results in restricted access to sensitive tissues.

As previously mentioned the solubility of a given cardenolide in the gut is an important factor in dictating the resultant concentration in the blood. Relatively lipophilic cardenolides have a greater potential to cross the gut and enter the blood stream (Parsons and Summers 1972, Megges and Repke 1963, Goodman and Gilman 1973, Okita 1967). If one analyzes the relationship between approximate polarity (based on TLC behaviour, partially a function of nuclear hydroxyl functions) of a cardenolide and that cardenolide's oral ED₅₀ (Table 1) it can be seen that the cardenolides that are more lipophilic (less water soluble) have generally lower dose requirements for emesis. It should be realized that this polarity relationship is a trend and not an invariable law; this also applies to R_f values, which can vary with solvent systems. Interestingly, emetic does (Table 1; M.E.D.), as determined by intravenous injections, shows that the polar cardenolides tend to be more effective

emetics. The reason the oral E.D.₅₀ of polar cardenolides is so low is that they pass poorly through the gut. It should also be noted that (Table 1) the intravenously determined lethal dose (M.L.D.) is much lower for polar cardenolides. I do not mean to imply that lethal dose and emetic dose are related phenomena. Unfortunately, most available pharmacological data is based on the cat, and thus for sake of argument the cat must be used as an artificial reference animal.

Table 1.—The potency of various cardenolides causing emesis or death in cats.

GLYC = cardenolide possess one or more glycosyl units at 3-OH position of steroid nucleus

OH = steroid nucleus, excluding butenolide ring, contains given number of oxygen functions.

M.L.D.= mean lethal dose; E.D.₅₀ = oral dose required make 50% of cats vomit; M.E.D. = mean emetic dose; i.v. = cardenolides given intravenously.

* Estimation of tendency to be polar or non-polar based on literature of TLC behaviour of cardenolides (Duffey, unpublished data; Parsons, 1965; vonEuw *et al.*, 1971; Rothschild *et al.*, 1973). The order of cardenolides approximates TLC behaviour, yet the relationships are not absolute.

** The toxicological data was derived from Parson, 1965; Hoch, 1961; Wilbrandt, 1963; Parsons and Summers, 1972).

Approxim. of Pol- arity Based on Functional Groups and TLC Data*		Toxicological Effects on Cat **			
		Trivial Names of Cardenolides	M.L.D. (mg/kg) by i.v.	ORAL E.D. ₅₀ (mg/kg)	M.E.D. by i.v. (mg / kg)
GLYC	OH				
+	5	HYDROPHILY	ouabain	0.11–0.15	2.5
	4		<i>α</i> - antiarin	0.13	0.06
	3		adonitoxin	0.19	
	3		convallatoxin	0.08	0.06
	3		cymarin	0.13	0.05–0.1
	2		sarmentocymarin	0.21	0.9
	2		lanatoside C	0.2	0.22
	2		digoxin	0.2–0.5	0.2
	2		stros peside	0.59	
	3		cymarigenin	0.30	0.1
+	1	TENDING TO	thevetin	0.8–1.0	0.3
	1		thevebioside	1.0	0.16
	2		digoxigenin	4.6	0.05
	1		digitoxin	0.3–1.0	0.2
	1		neriifolin	0.2	0.07 E.D. ₅₀
	1		oleandrin	0.2	0.1–0.3
	1		digitoxigenin	0.5	0.1–0.2
	2		calatropin	0.11	0.11
	2		calactin	0.11	0.06
	2		calatropogenin	2.6	0.06
-	2	LIOPHILY	uscharin		0.2
	2		uzarin	0.15	
	2		uzarigenin	4.5–5.0	0.3–0.5
	2		uzarigenin	1.0	
	1		digitoxigenin	0.5	0.1–0.2
	1		xysmalogenin	1.3	0.11
	0		acetyl-digitoxin	0.4–0.5	

A major factor which will affect emetic and lethal doses will be the ability of blood serum proteins to bind certain cardenolides. Studies on blood-binding potentials show that non-polar cardenolides like digitoxin, digitoxigenin and digoxigenin are bound effectively, while more polar cardenolides like digoxin and ouabain are poorly or negligibly bound (Beeck et al. 1972, Brock 1975, Detweiler 1967, Evered 1972, Kuschinsky 1969, Lukas and DeMartino 1969, Parsons and Summers 1972). This correlates with the lower intravenous effectiveness of relatively non-polar cardenolides as emetics. The solubility of various cardenolides in the fat pools could also be a factor in determining the extent and duration of pharmacological effects upon the predator (Okita 1967). The insensitivity of a predator to cardenolides might in part be related to the degree of inhibition that can arise in ATP-ase pump. Variations in the susceptibility of $\text{Na}^+\text{-K}^+\text{-ATPase}$ pumps amongst different animals has been shown to be dependent upon the kinetics of the inhibitory process. Animals with highly susceptible pumps tend to have more stable drug-enzyme complexes (Allen and Schwartz 1969, Tobin et al. 1972). In other words, the rate of dissociation of a cardenolide molecule from the drug enzyme complex is faster in somewhat resistant ATPase pumps.

Brower's studies on the palatability spectrum clearly demonstrated that *Asclepias syriaca* is unable to give rise to emetic butterflies; whereas, *A. curassavica* is able to produce emetic conspecifics (Brower et al. 1968). Also, the lygaeid *Oncopeltus fasciatus* when reared on *A. syriaca* seeds is palatable to toads; these toads will consistently eat 5 or more such bugs day after day with relish (Duffey and Scudder, unpublished data). Yet, if *O. fasciatus* is reared upon the seeds of *A. curassavica*, one bug is sufficient to produce regurgitation in toads, and the insect is subsequently refused as a food item for several days afterwards (Weber et al. 1976, unpublished data). How can this dichotomy of responses be explained?

The answer may lie in a superimposition of plant cardenolide chemistry and the insect's mechanism of sequestration. This last point will be discussed later. TLC analyses of both leaves and seeds of *A. syriaca* in comparison with *A. curassavica* reveal that *A. syriaca* have not only lower concentrations of cardenolides generally, but also either lacks or has very low amounts of relatively non-polar cardenolides like calactin, calatropin, uscharin, and calatoxin (Duffey and Scudder 1972, Parsons 1965, Reichstein et al. 1968, Roeske et al. 1975, Rothschild et al. 1975). Thus, when either *O. fasciatus* or *D. plexippus* feed upon plants like *A. syriaca*, they are presented with the opportunity to sequester emetic doses of the appropriate cardenolides. I argue that the most effective cardenolides for the induction of emesis are some of the above mentioned cardenolides, which are more available in species like *A. curassavica*. The basis for this argument has been partially discussed in reference to Table I where it was shown that non-polar cardenolides tend to pass through the gut more easily, but relatively more polar cardenolides tend to have lower dose requirements for i.v. induction of emesis. On this basis, calatropin and calactin, and perhaps other cardenolides of *Asclepias* spp., are peculiar because even though they are moderately non-polar (penetrate gut well), they also have much lower dose requirements to induce emesis once in the blood stream. Therefore, it might be that cardenolides like calactin and calatropin provide a fortuitous blend of amphiphilic physical properties, pharmacological potential, and propensity for being readily sequestered by insects. Perhaps, the cornerstone of cardenolide based mimicry complexes relies on the presence of these physically and pharmacologically distinctive cardenolides. For the sake of argument it might not be possible to base a mimicry complex reinforced by emesis with cardenolides such as ouabain, digitoxin or digitoxigenin strictly because there is a poor balance between oral and intravenous emetic potentials (Table I), unless the insect were to store several thousand micrograms.

Indeed, the number of cardenolides that can function as emetic agents in environment may be few in number as indicated by the floating figure in Fig. 2. This figure attempts to demonstrate that cardenolides, which are to function as emetic agents against predators, must have properties which permit storage in sufficient quantities in the insect (X-axis), have properties which permit efficient crossing of the gut of the predator (Y-axis), and have properties which minimize factors such as blood-protein binding (Z-axis). Perhaps, emesis as an environmentally effective means of reinforcing mimicry complexes is restricted to certain geographical areas in which plants provide cardenolides with the appropriate properties.

The implications of the above relationships are several for an insect that is relying upon inducing emetic behaviour in a predator. It can be considered, momentarily assuming all predators are equally responsive, that the insect must have the mechanism(s) to sequester sufficient quantities of one to many cardenolides such that effective gut penetration occurs, and low enough blood binding occurs so that emesis can result without causing death. In other words, there must be some balance

between the types of effective plant chemistry, the insect sequestration mechanism and the assumed response of the predator. If we interject the concepts that cardenolide-containing plants vary in their relative amounts and number of polar and non-polar cardenolides, that various insect species will vary in their capabilities to sequester different amounts and types of cardenolides from different plants, and finally that predators will vary immensely in their susceptibility and modes of susceptibility to types and amounts of cardenolides, we must conclude that the "palatability spectrum" is indeed a very poorly understood term. This above epithet in retrospect is perhaps a unfortunate choice since the term "palatability" (Brower et al. 1968) semantically suggests a process of oral discrimination; whereas, the estimation of the palatability spectrum was based on an emetic criterion, which is not a gustatory phenomenon. The assessment of the role of cardenolides as defensive constituents in insects cannot be described by merely observing the reactions of one or two putative predators, nor by extrapolating from one bioassay. I am unaware of any study that proves by field data, as opposed to laboratory data, that emesis is a natural phenomenon in a wild population of predators, and the sole physiological basis of reinforcing the forgetful or naive predator.

Various studies have shown that cardenolide containing plants vary considerably in content and type inter- and intraspecifically (Evans and Cowley 1972, Duffey and Scudder 1972, Roeske et al. 1975, Bleier et al. 1967, Rothschild et al. 1975). Moreover, the cardenolide content inter- and intraspecifically amongst insects also varies considerably (vonEuw et al. 1971, vonEuw et al. 1968, Rothschild et al. 1973, Rothschild 1972a, Duffey and Scudder 1972, Scudder and Duffey 1974). Also, the variation of response of a variety of predators to a given prey is certainly not without documentation (Marsh and Rothschild 1974, Rothschild and Kellet 1972, Rothschild 1966). Indeed,

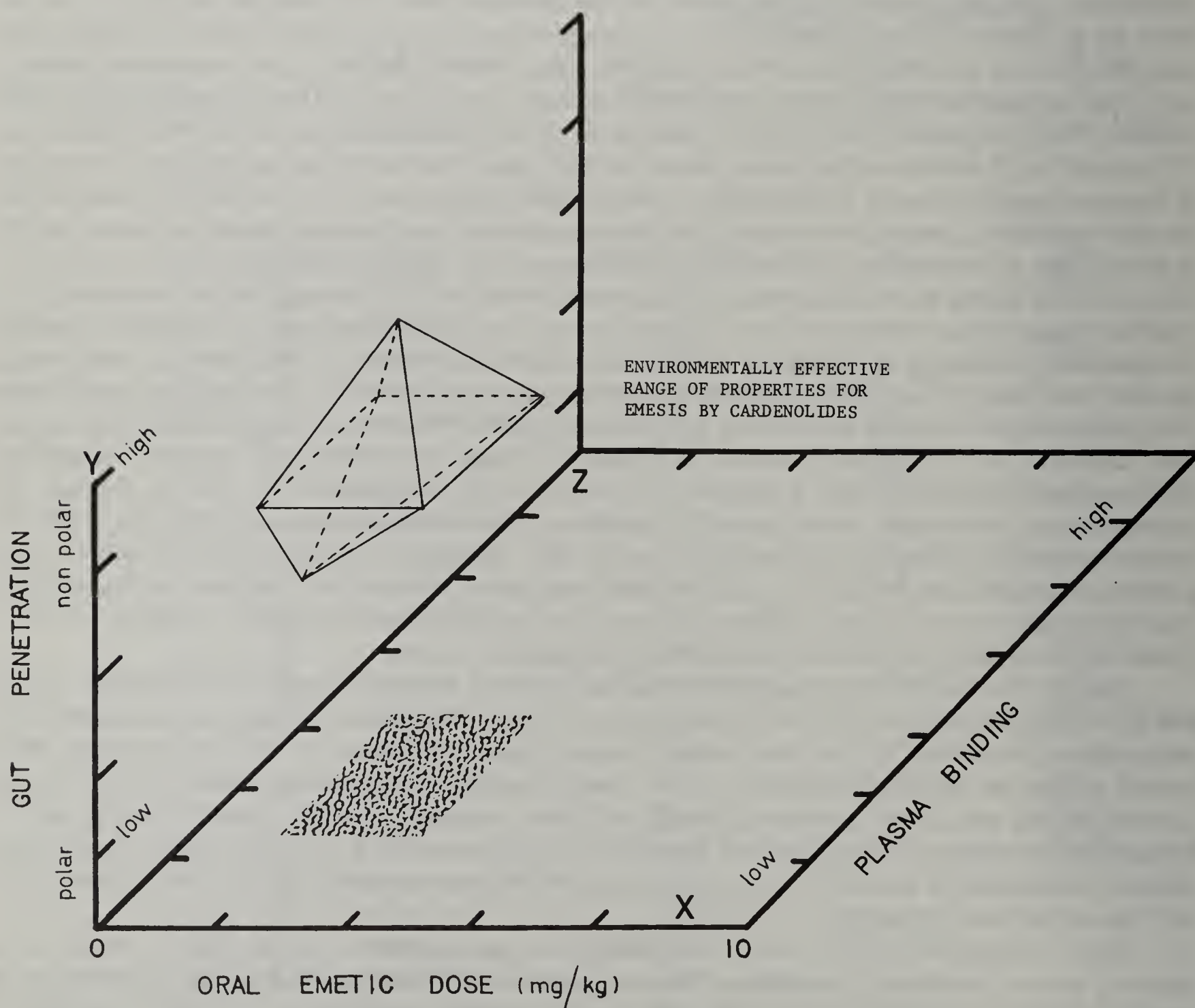


Fig. 2. —Some physiological factors of the predator that might alter the environmentally effective range of emetic cardenolides.

viewing the diverse biological activities of cardenolides upon vertebrates (Goodman and Gilman 1973, Lüllmann and Peters 1974, Taeschler et al. 1969, Thorp and Cobbin 1967) one can only be led to suspect that predators might learn to avoid members of a mimetic complex because of prior experience with a number of physiological stresses (distastefulness, indigestibility, vascular dysfunction, muscular distress, stomach spasms, nausea as examples) rather than by induced emesis. These possibilities need serious consideration.

In fact if one considers the evidence, it has not been unambiguously proven that the total cardenolide content, or the content of specific cardenolides of Monarch butterflies or any insects is alone responsible for the total emetic effect observed in jays or other predators. However, the work of Brower and Moffit (1974) has demonstrated that there appears to be a correlation between the gross cardenolide content of Eastern and Western Monarch butterflies and their emetic potential in jays. But it has yet to be proven that these insect do not represent a Galenical mixture of which cardenolides are only a portion of the chemicals inducing emesis. Rothschild et al. (1975) suggest this might be the case for certain African butterflies that contain cardenolides. A variety of other chemicals have the ability to induce emesis; salicylic acid (Clark et al. 1972), L-DOPA (Mori and Sakai 1971), and L-aspartic acid (Fleischman et al. 1973) as examples. *Asclepias syriaca* contains nicotine (Marion 1939); is this compound found in monarch butterflies?

Another important consideration is the concept of the word emesis. Pharmacologically, emesis can be specifically interpreted as a drug-induced vomiting response as a result of the drug acting upon some central nervous (Chai et al. 1972, Gaitonde and Joglekar 1972). As emesis is currently used in the mimicry literature (Brower et al. 1974, Rothschild 1966), it is assumed that any regurgitated prey represents an emetic response. This observation of regurgitation is not correlatable with an arbitrarily strict definition of emesis induced at a higher nervous center. In other words, since cardenolides have the ability to cause strong contractions in smooth muscle (Lüllmann and Peters 1974), what is described as emesis may merely represent gastric irritation or some related visceral phenomenon. Thus, regurgitation and emesis must be considered distinct processes. Rothschild et al. (1975) have distinguished between these two phenomena.

In essence, our understanding of the force of cardenolides upon predators is limited. The ability of given cardenolides to induce stomach contractions, rather than induce emesis, would mean that less cardenolide content per insect would be required. Aglycones (non-polar) and non-polar cardenolides are less effective at inducing immediate contractions in smooth muscle, than are polar cardenolides like ouabain (Wilbrandt 1963). It is possible to consider that an insect may in fact have fortuitously evolved two or more lines of defense against predators, one depending upon slightly delayed responses such as emesis, one upon a more rapid response like regurgitation or alimentary irritation, and possibly others based on more delayed toxic effects. Many cardenolides have very bitter tastes, yet no experiments seem to have been carried out to demonstrate that the presence of cardenolides in a variety of insects could be used as defensive mechanisms through their distasteful properties rather than through their potentially emetic properties.

Many additional factors may be found to be important, or many of the above concepts and criticism irrelevant, as determinants of the effectiveness of cardenolides as an antipredator device. Heuristic arguments have a value until proven or disproven. It is perhaps a depressing thought that most arthropod allomonal system may only be comprehended by diverse lines of interdisciplinary research. Herein lies the challenge.

Allomones and Antibiosis Against Microorganisms

The antibiotic properties of arthropod allomones

The fossilized remains of a *Triceratops* easily conjure visions of a bloody battle with a *Tyrannosaurus*. The visual impact of those defensive horns intensified by fantasy dramatically convey the peril of the *Triceratops* while defending itself against such a macro-predator. The drama of our imaginations can be so intent upon this *momentary* battle that it is easy to forget that the *Triceratops* is continuously under seige by a variety of *micro*-predators — the worms, the fungi, the bacteria, the protozoans, *et cetera*. So it is with arthropod allomones.

The often visually impressive release of quinones by millipedes or beetles, defensive froth by some grasshoppers, or odiferous secretions by hemiptera for example focuses attentions too much

upon the deterrence of large predator. The result of this, of course, is that the literature on arthropod allomones is imbalanced by a plethora of instances of allomonal deterrence of macrobes, and a paucity of examples of allomonal antibiosis of microbes. It is puzzling why this state should exist. The literature on suspected allomones in plants related to disease and insect attack is replete (Atsatt and O'Dowd 1976, Beck 1965, Chapman 1974, Chou and Young 1975, Deverall 1972a, 1972b, Feeny 1975, Heftman 1975, Hutchinson 1973, Janzen 1975, Kuć 1975, 1972, Maxwell et al. 1972, Mitscher 1972, Rehr et al. 1973b, Schafer 1971, Schoohoven 1972, Stoessl 1970, Thorsteinson 1960, Whittaker and Feeny 1971). The view that arthropod allomones might function as antifungal, or antibacterial agents was discussed many years ago by Roth and Eisner (1961). It was known at for example this time that simple benzoquinones *in vitro* had the ability to interfere with the growth of certain bacteria (DeCoursey et al. 1955, Estable et al. 1955). Several other examples are cited by Roth and Eisner (1961) who incidently point out that the suggestive value of these *ex situ* findings will only acquire relevance if they are substantiated by field data. Despite their exhortations proofs of the antibiotic roles has since either been non-existent or unconvincing.

There is reason to believe that many arthropod allomonal secretions contain components which in themselves or in admixture might have a potential to modify the microorganismal environment at least to the extent of reducing the severity of pathogenic attacks. It is an interesting coincidence that many of the frequently encountered arthropod allomones (*p*-hydroxybenzoic acid, phenol, hydroquinone, limonene, α - and β -pinene, 1:8-cineole, phenylethyl alcohol) are precisely some of the compounds suspected as allelopathic and phytoalectic agents in plant-plant and plant-microorganism interactions (Chou and Young 1975, Kuć 1975, 1972, Mitscher 1975, Rice 1974, Stoessl 1970, Whittaker 1970, Whittaker and Feeny 1971). Perhaps there is something unique about the chemical and physical properties of molecules like the above which in relation to certain (common ?) irritable features of a variety organisms make the production of these chemicals advantageous both as immediate effronteries and long-term antagonists.

The simple *p*-benzoquinones (e.g., benzoquinone, toluquinone, ethylbenzoquinone, 2, 3-dimethyl-benzoquinone, and 2, 3, 5-trimethyl-benzoquinone) have been implicated as antibiotics. Arthropods, like spiroboliform millipedes, are well adapted morphologically and behaviorally to utilize their benzoquinone containing secretions in this capacity. Almost every diplosegment has a bilateral pair of defensive glands which open to the exterior *via* small pores. The millipede has the ability to control the amount of exudate from each of these pores (see Eisner 1970). Hypothetically, the millipede at will could liberate aliquots of benzoquinone containing secretion into the microorganism ridden habitat, forest soil layers or rotting logs.

The chemical and physical properties of benzoquinones are suited for the antagonism of microorganisms. The moderate volatility of these chemicals provides the means to permeate soil both in the gaseous and liquid phase (see Fries 1973). A more compelling reason to view them as highly toxic materials is their chemical reactivity. It has been mentioned previously that most simple benzoquinones have the ability to form covalent bonds with SH, NH, and NH₂ functions as well as aromatic compounds (Fieser and Ardao 1956, Flaig et al. 1973, Hackmann and Todd 1953, Kuć 1972, Moxon and Slitkin 1972, Paul 1970, Rich 1969, Swaby and Ladd 1962). In soil, quinones have been reported to crosslink with NH₂ and SH functions of free proteins to produce a copolymer which reduces the biodegradability of organic materials to some microorganisms (Flaig et al. 1973, Kuć 1972, Paul 1970, Swaby and Ladd 1962). These chemical properties of benzoquinones suit them well for interacting with living tissues as well. Also, the defensive secretion of many millipedes contains not only several benzoquinones but also easily detectable quantities of the corresponding hydroquinones (Duffey and Blum, unpublished data, Schildknecht and Kramer 1962), as well as phenol or cresol in some instances (Duffey and Blum, unpublished data, Kluge and Eisner 1971). Simple phenols (e.g., catechol, cresol and hydroquinone) can also covalently condense with soil organic material. A mixture of *p*-benzoquinone and hydroquinone, under the appropriate conditions, will condense to form quinhydrone; this last chemical has been shown to have antifungal properties (Nair and Anchel 1972).

One then wonders if the discrete liberation of quinones by soil dwelling arthropods could alter the physical and chemical nature of the soil so that a variety of desirable and/or undesirable microorganisms could be modulated for the benefit of the arthropod. This feasibly could result in lessened chances of contacting diseases, especially those of the cuticle. In otherwords, some susceptible microorganisms could immediately succumb to the toxic effects of absorbed quinones, while more resistant species might be controlled by creating unfavourable substrates. An over-kill

approach, need not be taken to evidence antibiosis or biostasis. The action of these chemicals may be more subtle than causing death. Benefits can accrue for the arthropod through the influences of its allomones on growth rates, spore germination, fecundity, reduced virulence, interference with chemotaxis, and perhaps a variety of other factors.

A number of incidental observations further point to the necessity of a more detailed examination of the roles of quinones and related chemicals in the biology of arthropods. Some phenols and quinones (benzoquinone, hydroquinone, phenol, *m*- and *o*-cresol, pyrogallol) have antimitotic properties (Dustin 1963, Goldstein et al. 1969). Benzoquinone inhibits fly ovarian growth (antimitotic ?) (Mitlin and Borody 1958). Various naphthoquinones have been implicated in resistance to some fungal and bacterial diseases in a variety of plants (Goodman et al. 1967, Mitscher 1975, Muller 1970). An antibiotic, 6-methyl-naphthoquinone has been isolated from a fungus, *Marasimus graminum* (see Thomson 1971). This naphthoquinone, along with simple benzoquinones, has been shown to occur in the tenebrionid beetle *Agroporis alutacea* as a defensive secretion (Tschinkel 1972).

The defensive release of HCN and benzaldehyde by polydesmoid millipedes is an intriguing adaptation in the light of the notoriety of HCN as a deadly poison. The toxicity of HCN to a variety of organisms would suggest that it might be highly functional as an antibiotic of forest floor dwelling arthropods like polydesmoids. Also, a number of fungi, bacteria, and green plants are cyanogenic (Eyjolfsson 1970, Conn 1974, Hutchinson 1973, Jones 1972). Verification of the role(s) of HCN for cyanogenic organisms has not been without its ambiguities. *In vitro* studies with microorganisms have shown that HCN, among other things, delays spore germination and reduces radial growth of fungi (Hutchinson 1973). For years the release HCN by green plants has been ambiguously viewed as an antipredator device (see Jones 1972). As usual, the prevailing problem is to relate laboratory studies to the complex environment.

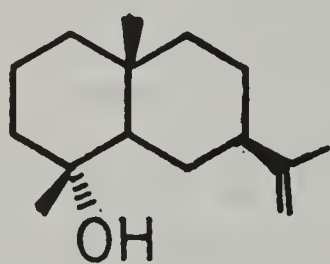
The polydesmoid allomones represent, like those of the spiroboliform millipedes, an ideal chemical and biological system for studying antibiosis. Recently, the secretions of a variety of polydesmoid millipedes like *Cherokia* spp. have been shown to be a complex mixture of organic molecules besides mandelonitrile, HCN and benzaldehyde. This mixture contains benzoic acid, mandelonitrile benzoate, and benzoyl cyanide as additional compounds (Duffey et al. 1976b). Laboratory investigations of the fungistatic properties of each of these chemicals has shown that they differentially inhibited spore germination and radial growth of hyphae of 14 species of forest litter fungi (Roncadori et al. unpublished data). When each of these compounds is considered on its own, the above (two) criteria of fungistasis are realized at concentrations of 250-1000 parts per million in the growth media. Benzoic acid was the most effective compound on both counts. The artificiality of this type of bioassay is realized when one assays the fungistatic properties of these chemicals as an admixture, which approximates the natural relative abundance of these chemicals in the millipede's defensive secretion. In this case the inhibition of both radial growth and spore germination in a large number of the species tested is synergized to the extent that a tenth as much of each individual component is needed to achieve equivalent inhibition. As similar fungistatic allomonal secretion was evidenced in polydesmoid millipedes that produce mixtures of HCN, benzaldehyde, phenol, guaiacol and ethyl benzoate (Duffey et al. 1976b, Roncadori et al. 1976, unpublished data).

These above findings reinforce my earlier argument, that an accurate assessment of the defensive capacities of allomones can only be achieved by considering the system as a whole. The biostatic properties of all these millipede allomones is equivalent to the fungistatic (40-1000 ppm) properties of citral (Cole et al. 1975). Citral was found to have differential antagonistic activity *in vitro* towards a variety of entomophagous and phytophagous fungi. Cole et al. (1975) also tested two other insect pheromones, 2-heptanone and 4-methyl-3-heptanone, for fungistasis (inhibition of radial growth and spore germination); both these chemicals were much less active than citral. Their data suggested that antifungal potency of citral against dermatophytes was equivalent to that reported for Amphotericin B. The activity of citral on these organisms was concentration dependent rather than time dependent. Unfortunately, the pertinent field data has not been derived. However, samples of forest litter exposed to a number of living polydesmid millipedes for several weeks, did not have the same microflora as unexposed forest litter (Roncadori et al. unpublished data). This points to the possibility of the millipedes actually altering the microorganismal composition of the adjacent litter. This has not been correlated with any data to demonstrate that the millipedes are continuously liberating small amounts of allomonal secretion in nature in order to modify the environment, not if

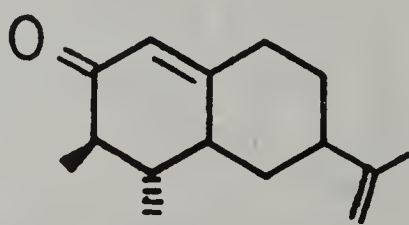
they do that this behaviour will confer an advantage upon them. It would seem that one prime objective in such an aseptic environment would be to maintain the integrity of the external cuticle.

Many arthropod allomonal systems have been the subjects of speculation concerning their antibiotic potential. Aromatic acids, like *p*-hydroxybenzoic acid or protocatechuic acid (Atkinson et al. 1973, Pryor et al. 1947), have been suggested to function as cuticular antibiotics (Gilmour 1965). Likewise, Schildknecht (1971) speculates that chemicals liberated as defensive secretions by water beetles (hydroquinone, *p*-hydroxybenzoic acid, protocatechuic acid, phenylacetic acid (*et cetera*)) work as antibiotic agents (Schildknecht 1971, Schildknecht et al. 1967a). In another example a leaf cutting ant *Atta sexdens*, besides producing its mandibular compliment of pheromones such as 4-methyl-3-heptanone (Blum 1969), secretes from its metathoracic glands L- β -hydroxy-decanoic acid, phenylacetic acid, and indolyl acetic acid. These three substances are claimed to aid the fungal-ant symbiosis by promoting the growth of the fungi (Schildknecht et al. 1973). It has been partially shown that phenylacetic acid and L- β -hydroxydecanoic acid can act *in vitro* as antibiotics against organisms such as *E. coli*, *Staphylococcus aureus*, and *Penicillium glaucum*. This antibiosis supposedly naturally maintains pure cultures of the fungus in the fungal garden (Maschwitz et al. 1970, Schildknecht 1971). The presence of indolyl acetic acid thus stimulates the growth of the fungi through an auxin-like effect (Schildknecht et al. 1973). This study does demonstrate that these secretions are stimulatory to the fungi, but their putative role in the natural milieu of the colony is far from established. These results are in contradiction with other work in attine ants and their fungi (Martin 1970, Martin and Martin 1970, Martin et al. 1969). It may be another coincidence that many male noctuids release isovaleric acid, benzaldehyde, 6-methyl-5-heptene-2-one, phenylethyl alcohol, and benzyl alcohol from their scent brushes (Aplin and Birch 1970, Birch 1974). The usual role assigned to these chemicals is a pheromonal one, despite the lack of behavioural data, and Birch (1974) further raises the point that perhaps some of these chemicals have antibiotic properties. Again, phenylethanol and benzyl alcohol have been implicated in plant allelopathy (Chou and Young 1975, Muller and Chou 1972, Rice 1976), 6-Methyl-5-hepten-2-one is also an alarm pheromone for several species of ants (Crewe and Blum 1971, McGurk et al. 1968, Travé and Pavan 1956). Interestingly, this chemical is an endogenous stimulator of uredospores of *Puccinia* rusts (Rines et al. 1974). Might not it be possible for such a chemical to control fungi in the ants nest or on the body by interfering with spore formation or other facets of the fungi's physiology?

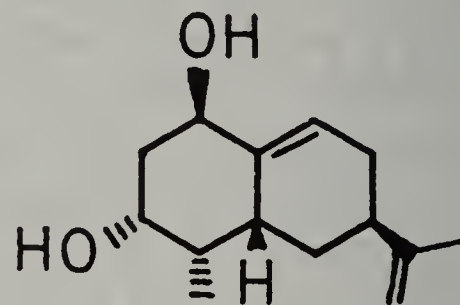
Another striking similarity in chemical defenses is observed between the papilionid butterfly *Battus polydamus* and the solanaceous plant *Nicotiana* sp. The butterfly secretes two major sesquiterpenes from its osmetrial defensive gland, one of which is sel-11-en-2-*a*-ol (Eisner et al. 1971b). When some species of *Nicotiana* are attacked by pathogens they produce a series of similar eudesmane sesquiterpenes, like glutinosone and capsidiol (Bailey et al. 1975, Burden et al. 1975, Deverall 1972a, 1972b, Stoessl et al. 1976), which have some antifungal and antiviral properties. Perhaps, further analyses of this butterfly secretion would reveal a diversity of sesquiterpenes that could feasible be employed by the insect to control microorganismal growth on its body or within the osmetrium.



Sel-11-en-2a-ol



Glutinosone



Capsidiol

Many arthropod allomonal systems are amenable to intensive study of their impact upon microorganisms. It is a pity that so few definitive or even suggestive studies have been undertaken. The data in Table 2 generally summarize some of the defensive chemicals of arthropods that have been implicated as antibiotics of plants against microorganisms. The data are not abundant, but they do suggest that there is just cause in suspecting that these compounds in arthropods might have subtle roles, just as it is apparent that the same or similar chemicals in plants have a spectrum of roles. In many cases we are dealing with chemicals that have significant degrees of *releaser* or *primer* activity in any biological context.

Table 2.—Antibiotics of plants found in arthropod defensive secretions, and allomones of arthropods with demonstrated antibiotic activity.

ALLOMONE	ORGANISMS AFFECTED	SOME ARTHROPOD SOURCES
<i>Plants</i>		
HCN	fungi & bacteria ¹	beetle, ² moths, ³ millipedes ⁴
Benzoic acid	fungi ^{5 6}	millipedes, ⁴ beetles ⁷
4-OH-Benzoic acid	fungi ⁸	beetles ⁷
4-OH-Benzaldehyde	fungi ⁹	beetles ^{7 10}
Cardenolides	bacteria, protozoa ^{1 1}	hemiptera, ^{1 2} butterflies, ^{1 3} grasshopper ^{1 4}
I:8-Cineole	bacteria ^{1 5}	beetles ^{1 6}
Citronellal	bacteria ^{1 7}	ants, ^{1 8} beetles ^{1 9}
Dihydromatricaria acid	fungi ^{2 0}	beetle ^{2 1}
Dimethyl sulphide	bacteria ^{2 2}	ants ^{2 3}
<i>trans</i> -2-Hexenal	fungi ^{2 4}	hemiptera ^{2 5}
Hydroquinone	fungi ^{2 6}	millipedes, ^{2 7} beetles ⁷
d-Limonene	bacteria ^{2 8}	termites, ^{2 9} ants ^{3 0}
6-Methoxy-mellein	fungi ^{3 1}	ants (mellein) ^{3 2}
6-Methyl-naphthoquinone	fungi ^{3 3}	beetle ^{3 4}
α and β -pinene	bacteria ^{1 7}	termites ^{2 9}
Protocatechuic acid	fungi ⁵	beetles ⁷
Corticosteroids	bacteria ^{3 5}	beetles ^{7 10}
<i>Arthropods</i>		
Benzoquinones	bacteria, fungi, protozoa ^{3 6}	beetles, ^{3 1} millipedes, ^{3 8 3 3} phalanaiids ^{3 6}
Benzaldehyde	fungi and bacteria ^{3 9}	millipedes ^{4 0}
Benzoic acid	fungi and bacteria ^{3 9}	millipedes ^{4 0}
Benzoyl cyanide	fungi and bacteria ^{3 9}	millipedes ^{4 0}
Citral	fungi ^{4 4}	ants ^{4 5}
Guaiacol	fungi and bacteria ^{3 9}	millipedes ^{4 0}
2- Heptanone	fungi ^{4 4}	ants ^{4 5}
L- β - Hydroxydecanoic acid	fungi and bacteria ^{4 1}	ants ^{4 1}
Mandelonitrile benzoate	fungi and bacteria ^{3 9}	millipedes ^{4 0}
4-Methyl-3-heptanone	fungi ^{4 4}	ants ^{4 5}
Phenol	fungi and bacteria ^{3 9}	millipedes ^{4 0}
Phenylacetic acid	fungi and bacteria ^{4 2}	ants, beetles, ^{4 2 7}
Sorbidomyristin	fungi ^{4 3}	aphids ^{4 3}

¹ Hutchinson, 1973; ² Moore, 1967; ³ Jones, 1972; Jones et al., 1972; ⁴ Duffey et al., 1976; Eisner and Eisner 1965; ⁵ Brown and Swinburne, 1971; Goodman et al., 1967; ⁶ Hubbes, 1969; ⁷ Schildknecht, 1971; ⁸ Fawcett and Spencer, 1968; ⁹ Fénical and McConnel, 1976; ¹⁰ Miller and Mumma, 1973; Schildknecht, 1971; ¹¹ Evanari, 1949; Heftman, 1975; Patton, 1974; Rice, 1974; ¹² vonEuw et al., 1971, Rothschild et al., 1970a; Scudder and Duffey, 1972; ¹³ Parsons, 1965; Rothschild et al., 1975; ¹⁴ vonEuw et al., 1967; ¹⁵ Roempp, 1966; ¹⁶ Schildknecht, 1970; Schildknecht et al., 1976; ¹⁷ Morris, 1972; ¹⁸ Chadha et al., 1962; Ghent, 1961; ¹⁹ Bellas et al., 1974; Kistner and Blum, 1971; ²⁰ Bohlmann et al., 1973; Drake and Lam, 1974; Mitscher, 1975; ²¹ Meinwald et al., 1968b; ²² Kadota and Ishida, 1972; ²³ Casnati et al., 1967; Crewe and Fletcher, 1974; ²⁴ Major et al., 1960; ²⁵ Calam and Yeudeowei, 1968; Waterhouse et al., 1961; ²⁶ Kuć, 1972; Nair and Anchel, 1968; Stoessl, 1970; ²⁷ Duffey and Blum unpublished; Happ, 1968; ²⁸ Murdock and Allen, 1964; ²⁹ Moore, 1968; Schildknecht et al., 1976; ³⁰ see Weatherston and Percy, 1970; ³¹ Kuć, 1972, ³² Lloyed et al., 1975; ³³ Thomson, 1971; ³⁴ Tschinkel, 1972; ³⁵ Heftmann, 1975; ³⁶ DeCoursey et al., 1953; Estable et al., 1955; Kuć, 1972; Nair and Anchel, 1968; ³⁷ Eisner et al., 1971; Tschinkel, 1975; ³⁸ Kluge and Eisner, 1971; Thomson, 1971; ³⁹ Roncadori et al., 1976, unpublished data; ⁴⁰ Duffey et al., 1976; ⁴¹ Schildknecht et al., 1973; ⁴² Maschwitz et al., 1970; ⁴³ Bowie and Cameron, 1965; Callow et al., 1973; Shimiza, 1971; ⁴⁴ Cole et al., 1975; ⁴⁵ Blum, 1969; Brand and Blum, 1972.

The quality of secretions

The argument to this point has considered that the functions of arthropod allomones are to ward off the momentary attacks of larger predators, as well as to assuage the perpetual attacks of microorganisms. There have been at least two implicit assumptions in these arguments; one, that the chemical composition of the secretion is constant in time, and two, that defense operates as an external phenomenon relative to the secretor. These assumptions may be true, but they bear analysis from the viewpoint of plant defences.

Plants, as they mature often show seasonal and age-related fluctuations in the amounts and types of “secondary” compounds (allomones?) present in various tissues (saponins, cyanogens, cardenolides, alkaloids, phenolics, alkaloids; Deverall 1972a, 1972b, Feeny 1970, Levin 1976, 1971, Feeny 1975, Seigel and Price 1976). In some instances, one or many of these fluctuations is correlatable with environmental stress (physical or biological). It is argued that “secondary” compounds whether they fluctuate or not, fulfill subtle physiological roles, but also act as protective investments against disease and predators. This chemical preparedness is viewed as *constitutive* defence. Plants also exhibit chemical changes which are concurrent with attack by pathogens. These changes are suspected of providing further resistance to the occurrence of extensive disease. Most often the pathogenic attack results in the accumulation, in organs or diseased regions of the plant, of several chemicals with *in vitro* have substantial antibiotic properties. This *post facto* response is termed *induced* resistance (Kuć 1972, Levin 1971).

Terrestrial arthropods are subject to many of the same physical and biological stresses endured by plants. In view of the opinion that arthropods and plants are often utilizing identical compounds as extrinsic modifiers of the environment, it might be feasible to suppose that an arthropod may also show seasonal variations in the quantitative and qualitative composition of its secretion (constitutive resistance), but also may show variations in composition as a result of disease (induced resistance).

Has chemical variation in an arthropod defensive secretion been documented? It has, but to a very limited extent. To quote from Waterhouse and Gilby (1964) — “It was found that the relative proportions of constituents in some species varied quite markedly at different times of the year and also in samples from different localities. For, example a sample from a single female of *Amorbus rubiginosus* collected in Autumn at Mossy Point, New South Wales, had more acetic acid and hexenal (a total of 40 instead of 25 percent and less hexanol (2 instead of 4 percent) and hexyl acetate (58 instead of 71 percent) than the bulk sample obtained from about 100 bugs collected in Canberra during the summer”. Yet, in another study of cockroaches (*Polyzosteria* spp.; Wallbank and Waterhouse 1970) found little variation in the relative abundance of *trans*-2-hexenal, and hex-2-enol of *P. limbata* after being successively milked of its secretions for six weeks. Also, the six species investigated showed very little variation in the chemical quality and quantity of their secretions.

However, Macloed et al. (1975) reported that the quantity of *trans*-2-octenyl acetate in the bug *Musgraevia sulciventris* varied considerably with season; whereas, the same chemical in the bug *Birorulus bibax* did not. In a comprehensive study of the chemical secretions of tenebrionid beetles Tschinkel (1975a) found that the variation of several quinones and alkenes in a given species of *Eleodes* (3 studied) from one locality was as great as the variation found in the beetle from different localities. He pointed out that these findings may be biased by sampling populations in localities too proximate. Nevertheless, both qualitative and quantitative interspecific variations in the chemical composition of these secretions were found in a variety of related tenebrionids (Tschinkel 1975a). The defensive pygidial secretions of four species of cychrine beetles, *Scaphinotus*, were found to contain a mixture of methacrylic and tiglic acids (Wheeler et al. 1970). A comparison of the relative abundance of these two components in the secretions of feral beetles showed considerable interspecific variance; however, the reliability of these determinations based on insects of unknown histories was questioned by the authors because they observed dramatic changes in the relative abundance of each component in insects that had been held in captivity. For instance, *S. viduus* had 99% methacrylic acid and undetectable amounts of tiglic acid in freshly collected beetles, yet after 3-6 weeks in captivity, the relative abundance had switched to 15 to 85% respectively. The authors suggested that diet might be the factor determining this distinctive change. Whether this is really the case is of secondary importance to their admonition that “caution should be used in characterizing species by the composition of their defensive secretion”. The larvae of the papilionid butterfly *Papilio*

aegus show a very interesting secretory adaptation. The osmetrial gland of the 4th (last)-instar secretes isobutyric acid, while the osmetrium during the 3rd-instar only liberates β -hydroxybutyric acid (Seligman and Doy 1973). The significance of this adaptation or any of the above variations in the biology of the arthropod is unknown.

At present there is no body of data which permits an explanation of these phenomena. Such fluctuations in allomonal chemistry may merely be the result of age dependent processes. Yet, it is more tempting to speculate that in some cases they are related to temporal changes in the types of predators and pathogens (in hemiptera at least, one must also account for communicative roles). Thus, by temporally varying the composition of the secretion the prey might be attuning itself to the susceptibilities of certain foes. It is also possible that a variation in composition could arise as an induced phenomenon in response to the stresses caused by developing diseases or parasites. Many more ecological explanations are possible, and few if any have been explored.

Most arguments for the roles of arthropod allomones focus on the external adversities of that organism. This leaves in limbo the internal environment of the arthropod, which is a haven for bacteria, protozoa, fungi, nematodes, and other parasitic organisms. The intussuption of these latter organisms into the body of an arthropod is known to induce a variety of physiological and biochemical changes that are correlatable with cellular defensive reactions (Maramorosch and Shope 1975, Salt 1970) (antibiosis, encapsulation, sclerotization, phagocytosis, melanization). Would it not be possible for an arthropod that stores, for the sake of argument, benzoquinones, the corresponding hydroquinones and their glucosides, and several simple phenols in a glandular apparatus, to use these potentially antibiotic compounds as an internal defence mechanism? Although it is obvious that defensive glands segregate the defensive liquid from the internal organs, it has not been clearly established that this is the only site of residence of these molecules. Some of the more water soluble allomones may actually be present in "non-glandular" tissues as a constitutive defense; or upon invasion by foreign organisms an induced accumulation of some of these chemicals could occur in the haemolymph or infected tissues. Substances like cantharidin (Carrel and Eisner 1974) may have a number of fundamental functions besides being a blood borne factor designed for enhancing defense by reflexive bleeding. Plants are known to localize hydroxy fatty acids in their cuticle (Kolattukudy 1970), and some plants deposit the bulk of chemicals like nicotine, theine, and diosgenin in the epidermis or outer cell layers of the vegetative organs (McKey 1974). The tanning process of cuticle essentially localizes phenolic compounds to the exterior; this may represent a fortuitous combination of chemicals possessing not only the chemical reactivity to form a copolymeric cover but also advantageous toxicological properties. Do insects localize other potentially toxic agents in their cuticle or other organs?

The reasons for the inter- and intraspecific variations of chemical types found in the defensive secretions of taxonomically related arthropods provide another set of problems worthy of investigation. As mentioned above, Tschinkel (1975a) has demonstrated large interspecific and intergeneric differences in the chemical composition of 147 species of tenebrionid beetles from 55 genera. Some of the chemicals which could occur in a given secretion were benzoquinone, toluquinone, 2-methoxy-3-methyl-benzoquinone, ethylbenzoquinone, *n*-propyl-benzoquinone, octanoic acid, 1-nonene, 1-heptadene, 1-pentadecene, 1-tridecene, and 6-alkyl-naphthoquinones. The allomonal system of these tenebrionids is perhaps an ideal one to begin investigations of the full environmental significance of these compounds, because a reasonable amount of behavioural, morphological taxonomic, and ecological information is already known about these organisms (Doyen and Somerby 1974, Doyen and Tschinkel 1974, Tschinkel 1975a, 1975b, 1975c, 1972).

Another example of diversity at the inter-generic level occurs in staphylinid beetles (Table 3). How and why did such interspecific chemical diversity evolve? Why are different glands employed in different beetles (Table 3)? Can any of these chemical characters be related to different stresses present in a variety of habitats? We know nothing about these fundamental issues!

The chemical complexity of secretions

The question can also be asked: why do some arthropods evolve such chemically complex defensive secretions? In *Iridomyrmex humilis* over 55 chemical species have been identified (Cavill and Houghton 1974). Tschinkel (1975a) reports that *Eleodes beameri* secretes at least 23 compounds. The Jamaican millipede *Rhinocricus holomelanus* secretes at least 15 other chemicals along with 4 or 5 simple benzoquinones (Duffey et al. unpublished data). Many more examples can be cited. It is

Table 3.—The Chemical Diversity and Glandular Origin of
Staphylinid Beetle Defensive Secretions

BEETLE	CHEMICALS	GLANDULAR SOURCE	AUTHORITY
<i>Stenus coma</i>	1:8-cineole isopiperitenol 6-methyl-5-ene-2-one N-ethyl-3-(2-methylbutyl)- piperidine	pygidial	Schildknecht et al., 1976
<i>Drusilla canaliculata</i>	benzoquinone toluquinone 2-methoxy-3-methyl-benzoquinone 2-hydroxy-3-methyl-benzoquinone (corresponding hydroquinones) <i>n</i> -dodecenal <i>n</i> -tetradecenal <i>n</i> -tetradec-5-enal <i>n</i> -tetradeca-5,8-dienal	tergal	Brand et al., 1973
<i>Bledius spectabilis</i> <i>Bledius mandibularis</i>	neral geranial α -dodecalactone benzoquinone 1-undecene	pygidial	Wheeler et al., 1972a
<i>Staphilinus olens</i>	iridodial 4-methyl-hexan-3-one	tergal	Abou-Donia et al., 1971 Fish and Pattenden, 1975
<i>Thyreocephalus lorquini</i>	citronellal iridodial <i>iso</i> -valeraldehyde actinidine geranial	pygidial	Bellas et al., 1974
<i>Stenus bipunctatis</i>	1:8-cineole isopiperitenol 6-methyl-5-en-2-one	pygidial	Schildknecht, 1970
<i>Pella japonica</i> *	citronellal (incomplete)	tergal	Kistner and Blum, 1971
<i>Lomechusa strumosa</i> *	benzoquinone toluquinone ethylbenzoquinone <i>n</i> -tridecane <i>n</i> -tridecene	tergal	Blum et al., 1971

*Myrmecophilous

likely that detailed reanalyses of many defensive secretions, previously analyzed for only major components, will be shown to be highly complex mixtures.

Several reasons have already been offered to explain why a high degree of chemical complexity in an allomonal secretion may be advantageous for an arthropod. It was argued that a secretion containing a variety of chemicals might have the potential to play upon a greater number (or at least one) of physiological susceptibilities of the predator, as well as possibly to provide a similar buffer against a larger spectrum of foes. The predator population should then not so easily evolve a tolerance of resistance to the chemical complexity of one species of prey, let alone an immunity to the chemical complexities presented by a multitude of prey species. One additional feature of an allomonal secretion, which can be varied with time, is its quantitative and qualitative composition. The introduction of this factor into predator-prey relationships produces a dynamic system, which should make it even more difficult for a predatory population to gain the evolutionary "upper hand". This line of reasoning has applied to "plant defense guilds" as a mechanism of resistance against herbivores (Atsatt and O'Dowd 1976). The essence of their argument is that the conservation of both susceptible and resistant plant genotypes, the ratio of which vary's in time, produces a system of such variability and complexity to herbivores that the evolution of a virulent strain of herbivores is minimized. The presence of susceptible plant genotypes permits the existence of herbivores that are genotypically more sensitive to the plant quality. Thus, "the concept of gene conservation guilds adds diversionary and delaying tactics to the adaptation-counter adaptation view of plant-herbivore coevolution". If this argument is applicable to the allomonal systems of arthropods, it can be envisaged that behavioural, morphological, and chemical complexity in defensive strategies might be of prime importance in the survival of insect populations, especially mimicry complexes.

It might be worthwhile to consider that many arthropod allomones may in an evolutionary time scale be advantageous for a predator. Brown's definition assumes that no benefit accrues for the foe who is built to be repulsed by the given immediate or delayed effects of another organism's allomones. If long range detrimental effects occur from the ingestion of some allomones then perhaps it is advantageous for certain predators to avoid eating such prey by evolving a high intolerance to the immediate effects of the allomones (stench, irritation, taste). If this is the case, then the original definition of the word allomone may be in need of revision.

Physical and miscellaneous functions of allomones

The solvency of an allomonal secretion on biological tissues as a factor enhancing its efficacy has already been discussed. One additional point remains to be made concerning the advantages of chemically complex secretions in terms of solvent effects and eventual toxicity. Assume that an insect copiously secretes hex-2-en-1-ol, hex-2-en-1-ol acetate, and *n*-tridecane. It is arguable that *n*-tridecane is the carrier solvent which assists the penetrant properties of the acetate, both of which in turn have rendered the target tissue available to the potentially irritating and or toxic effects of hex-2-en-1-ol. The implicit assumption is that all predators have tissues with similar physical properties. In other words, *n*-tridecane as a penetrant may be irrelevant to an attacker with a hydrophilic mouth or skin (aquatic organisms?), and in fact it may be the more polar hex-2-en-1-ol which is the penetrant and toxicant. Similar permutations may be made for a variety of predators with different skin, cuticle, or membrane properties. Thus, by evolving a secretion that contains chemicals ranging from relatively polar to non-polar solvents, the chances of one to several of the components being successful in dissolving in the tissue or cells of the attacker may be greater.

The same argument may be applied to plant defense against herbivores. The toxic or deterrent affects of some molecules may be enhanced by storing them, say, in the form of more polar glycosides, peptides, salts, and halides as well as in less polar forms as aglycones, esters, and ethers. Sucking hemiptera would be more likely to absorb saliva soluble (polar) compounds from plant tissue than more non-polar derivatives. Some hydrolysis might occur by salivary and alimentary enzymes which would produce less polar compounds with greater propensities for penetrating the gut wall. Yet, the possession of non-polar chemicals would also equip the plant with readily gut-soluble toxicants for grazers.

Pharmacologists very often use the non-polar nature of many drug derivatives to aid gut penetration, after which hydrolysis or enzymic activities converts the "prodrug" into an active agonist or antagonist. It is conceivable from this standpoint to postulate that many allomones (hex-2-en-1-ol acetate) might operate in this manner. Their own solvent properties or those of the

carrier permit effective entry of the prodrug into the attackers tissues. At the original site or in target tissues metabolic conversion occurs (hex-2-en-1-ol) and toxic effects or irritancy are achieved which would not otherwise be realized. The presence of mandelonitrile benzoate in the cyanogenic secretions of certain polydesmoid millipedes (Duffey et al. 1976b) many function as a prodrug, since the chemical itself has no apparent repulsive properties to predators. Its very non-polar nature may aid its entry into microbial or macrobial tissues, after which esterase activity could liberate labile mandelonitrile and subsequently HCN and benzaldehyde. Depending upon the distribution of the benzoate in the organism the toxic effects of HCN and/or benzaldehyde could be more severe than if encountered internally in this form. A variety of arthropod allomones could function in this capacity when in contact with the right attacker; ethyl benzoate, methyl homogentisate, aliphatic ester, or aldehydes as examples. Auto-toxication is another facet of the absorption and metabolism of foreign chemicals.

Viewing the ability of a series of defensive chemicals to penetrate skin, cuticle, or cell membranes as a simple function of polarity, akin to an elutropic series (see Stahl 1969) is too simplistic. Experimenters often topically apply hormones or insecticides to insect cuticle in non-polar solvents like hexane, or olive oil, or even amphiphilic solvents like acetone. These solvents, although they dissolve in the cuticle do not destroy the integrity of the cuticle when applied in moderation. What physical qualities of a solvent (allomone) besides lipophily versus hydrophily could be used to index not only its penetrant but also destructive qualities? Parameters like ionic strength, dipole moment, dielectric constant, or other inherent physical properties may be critical factors.

As a further example, *n*-hexane is non-polar, non-ionic, has both a low dielectric constant and a small dipole moment, and will penetrate cuticle or membranes; but it will not destroy their integrity when applied in small amounts. However, chemicals like the Tween series, Triton X, and other non-ionic and ionic detergents are relatively non-polar, have variant dipole moments and dielectric constants and yet have the potential to lower the interfacial surface tensions of organic structures, membranes. Good wetting agents are not always good detergents. One can not strictly correlate this penetrant and/or surfactant property to any one of the above physical parameters, for though they can be mutually exclusive, they may also cooperatively lend to surfactancy or detergency. The problem physical chemists face is to explain via an unified theory how such a variety of chemicals can produce micelles and emulsions (Tanford 1973, Shaw 1966). I am not recommending this severe an analysis for arthropod allomones. Yet, it might be highly profitable for biophysicists to derive some basic data as to how the physical properties of allomones might be suited for penetration and emulsification of tissue. Some of the above parameters may be important. Perhaps it will be found that the evolution of allomonal secretions has in part been directed by their physical relevance to attackers. It is too easy to glibly refer to penetrants or spreading agents; these qualifications can be inexactitudes like the words detergency or repellency. It is perhaps unfortunate the words repellent or repulsive are used to describe prey-predator interactions, when they can be used in a physical sense to describe non-attractive forces between chemicals and particles.

The physical properties of allomonal secretions in a multitude of ways can also affect their liberation and storage. The viscosity of the defensive secretion will be one determinant of the rate at which an arthropod can propel or exude this fluid from a small external glandular orifice. This factor becomes even more critical if the secretion has to pass along a narrow tube before expulsion. This is the case in polydesmoid millipedes like *Cherokia georgiana*, where the mandelonitrile containing secretion must first pass along the narrow neck of the storage chamber (approx. $30 \times 100 \mu\text{m}$), through the reaction chamber, and eventually along another narrow tube ($30 \times 50 \mu\text{m}$) before passing out the orifice. In some millipedes, this last tube leading from reaction chamber to the orifice is quite long ($60 \times 200 \mu\text{m}$) (Duffey and Curzon, unpublished data). The internal haemostatic and/or muscular pressure required to drive a volume of fluid to the exterior is a direct proportion of the length of the tube and the viscosity of the fluid, but an indirect function of the cross-sectional area (actually πr^4) of the tube. Supposing that *C. georgiana* secretes pure mandelonitrile, it can be calculated that a pressure of 1-10 thousand dynes/cm² would be required to expel a volume of mandelonitrile ($30 \times 200 \mu\text{m}$) in about 1 second. In this instance the viscosity of mandelonitrile is 8.2 centipoises.

However, *C. georgiana* secretes mandelonitrile in admixture with other compounds (Duffey et al. 1976b). By mixing mandelonitrile, benzoic acid, mandelonitrile benzoate, and benzoyl cyanide together in the approximate ratio observed in the animal, it was found that the viscosity of the fluid fell to approximately 4 centipoises (Duffey and Blum, unpublished data). This decrease in viscosity

would enable the animal to utilize less internal pressure to propel the same volume of liquid in the same time (Duffey and Curzon, unpublished data). The surface tension of this admixture appeared to remain the same (32 dynes/cm). It would be most interesting to have good comparative data on the morphological design of high and low velocity glandular apparatus, coupled with physical data to indicate whether there has been a selection for low viscosity secretions, and whether in fact those secretions represent optimal chemical mixtures, compared with other natural or artificial mixtures. Also, depending upon whether an insect had evolved a mechanism to ooze liquid or produce fine sprays, one might expect to find specific chemical components of the secretion which increase or lower the viscosity to achieve these ends.

The surface tension properties of an allomonal secretion are also of prime importance in the internal maintenance of the liquid as well as in its effective presentation to the foe. Interfacial surface tension between glandular structures or glandularly contained water will partially determine the form of the organic phase (emulsion, droplets, one droplet, solution, micelles), and the position it occupies in the storage chamber of the gland (adhesion or non-adhesion to glandular surface). In defensive glands which pass their products from the secretory cells via fine capillary tubes to larger storage areas (Eisner et al. 1964, in *Eleodes longicollis*) it might be advantageous to evolve a secretion and/or a capillary lining which gives rise to wetting so that a positive meniscus is obtained, otherwise pressure is required to move the secretion into the storage area.

In other arthropods, which evert or only internally compress highly deformable sacs, surface tension (in relation to external cuticle surface properties) should be an important factor in determining whether the fluid spreads over the surface of the liberator or remains localized and subject to retrieval. Likewise, surface tension of defensive liquids and the mushroom-like structures of evaporatoria in hemiptera are inter-related phenomena (Hepburn and Yonke 1971, Remold 1963). This inter-relationship provides an elegant means of localizing the secretion to a specific portion of the body. The cardenolide containing secretion of the grasshopper *Poekilocerus bufonis* (vonEuw et al. 1967, Reichstein 1969) is ejected as a foam onto the abdomen. Besides the morphological adaptations (e.g., correct positioning of air injecting trachea), what chemical and/or physical adaptations of this secretion permit it to be such an effective foam (yet not spread)? Viscosity and surface tension will be factors in determining the extent and life of the form. Is the secretion actually an emulsion, which would favour foaming upon air injection, or are there other chemical factors that contribute a high degree of surfactancy rather than detergency (the secretion does not spread over the whole insect)? *Foam* is epithetical like *deterrency*; both describe immensely complicated phenomena of which there are a multitude of undescribed facets. Unfortunately, quantitative studies of the above phenomena are lacking, especially in a comparative degree.

If the defense of the external cuticle of arthropods can be accomplished through the antibiotic properties of allomonal secretions, one might also suspect the secretion to have detergent properties. Perhaps there are agents in defensive secretions which are able to spread as a monomolecular film over the cuticle and in this process scrub the cuticle free of small encrusting particles (see Shaw 1969). In this case, the arthropod would continually need to utilize its defensive glands as a "pipetting machine". Tschinkel (1975b) describes the elytra of several tenebrionid beetles as being morphologically well suited for the spreading of quinone containing liquid over and under the elytra. This may not only be highly adaptive for defense against large predators, but would certainly also facilitate cleansing and antibiosis. Schildknecht (1971) alludes to properties of phenolics, glycoproteins, and water beetle cuticle, which together provide the insect with a putative antimicrobial shell. Many terrestrial defensive secretions have proteinaceous components, which if like lipoproteins (Shaw 1969), could enhance the detergency. Along similar lines, the Queensland fruit fly, *Dacus tyroni*, (Evans and Stanbury 1967) has paired glands on one abdomonal tergite which releases both an aqueous and waxy secretion. This fly cleanses itself by wiping the secretions from these glands over his body; this activity reduces water loss. It would be interesting to know in this case whether these secretions have enough surface activity to also cleanse the cuticle. Any of the above organisms would be ideal to test the hypothesis of detergency and antibiosis with adroit physical and biological experiments.

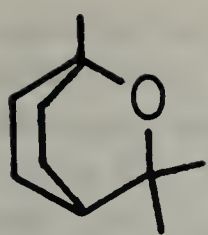
Many allomones and pheromones evaporate within a short time after emission. This evaporatory rate is a complex function of the chemical and physical properties of that secretion. We know very little of the interactive affects of these defensive chemicals which in admixture can increase or reduce the evaporative rate of the total secretion. In other words are there any common chemical and/or physical qualities of secretions that have been selected for in arthropods that rely upon increased or

decreased evaporatory rates of specific components for defence against predators or for communication? It is known that the presence of alkanes or alkanols, with higher boiling points than the more volatile components of pheromonal secretions, can significantly reduce the evaporatory rate of the volatiles (see Blum 1969, Wilson 1970). This suppression of evaporation need not rely on admixture with higher boiling range compounds, nor in all cases may this be the appropriate explanation. It is equally feasible to consider that chemicals which increase hydrogen bonding, electrostatic attraction, surface tension, or perhaps cause a variety of other physical changes could detain volatile molecules in a solvent. The mere fact that the mole ratio is altered by admixture can be suppressive. Likewise, an increase in evaporatory rates could be realized by low surface tension, little hydrogen bonding, low electrical attraction, azeotropic effects, and even association with solvent molecules that are globular rather than linear in shape. Are any of these phenomena important determinants of the efficacy of defensive and pheromonal secretions? The importance of understanding the physical details of how allomonal secretions function is equivalent to the importance of understanding in what manner allomones and pheromones are perceived by the receiver. The search for this knowledge will require interdisciplinary expertise.

In what ways can various components of arthropod liquid defensive secretions aid in the glandular storage? This question has virtually been unexplored. Can chemicals like *n*-tridecane or *n*-dodecanone, which might otherwise be viewed as carriers, effect the sequestration of other organic components produced by the secretory cells? This could be accomplished by providing a physical sink wherein the partition coefficient grossly favours their accumulation in the solvent as opposed to the cellular components. Certain chemicals may dictate whether a secretion is a biphasic, an emulsion, made of micelles, or under the appropriate agitation, a foam. The types of chemicals that are present will determine the stability of biphases *et cetera*. This may actually be important in defensive secretions which arise from several distinct morphological portions of a glandular system. In fact, the insolubility of many allomones in hydrated biological tissues or body fluids may provide a mechanism for the accumulation of these allomones in the glands. If the secretory cells liberate allomones to their exteriors into an aqueous fluid to their limits of solubility it might be possible for phase formation to occur (Gibbs phase rule). Once this occurs a physical equilibrium is enstated so that free concentration of the allomone is fixed while all additional allomone enters into the phase. Such a process might be invoked to explain how saw fly larvae (*Neodiprion*, Eisner et al. 1974b) sequester plant resins in their alimentary diverticula. Certainly, no body of evidence is available to bias one's views towards the totally active accumulation of allomones in glands, although arthropods will probably be found to employ a variety of mechanisms for accumulation of allomones in glands.

Many allomonal chemicals are highly reactive molecules. The benzoquinones are not particularly stable molecules when exposed to air, and have the potential to react with a variety of compounds. How might an arthropod that stores these chemicals stabilize the secretion in the glandular storage area so that it does not react with bodily tissues or other components in the defensive secretion? One means is to present a physical barrier such as, preferentially permeable cuticle on the lumen of the gland; supposedly some chemicals can be placed in the lumen initially by passing through cells as a glycoside whereupon it is hydrolyzed to a non-permeating chemical at the lumen interface (Happ 1968, Clearwater 1975a, 1975b). Another means, which can be coupled with the above process, is to include free radical inhibitors such as phenol, cresol, hydroquinone, or cysteine. These chemicals are common components of quinone-bearing secretions. Perhaps, a major role for these chemicals is to chemically stabilize the components of the secretion. This need not apply to all secretions. Are there any chemical factors, besides approximating a neat liquid within the gland, that enable polydesmids to store the highly labile mandelonitrile? None of these facets have been examined.

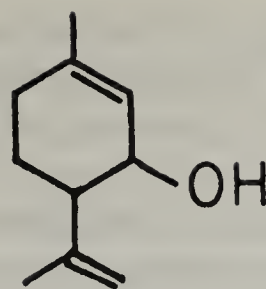
The importance of the physical properties of allomones in defense is not without some specific documentations. The super-cooling of the cornicular droplets of aphids represents an interesting utilization of a non-chemical process (Dixon 1958, Edwards 1966) as a defensive mechanism. More intriguing in its simplicity is the combination of allomonal activity against predators with *Entspannungsschwimmen* (propellency across water) from the secretions of some water beetles (*Stenus coma*; Schildknecht et al. 1976). This staphylinid beetle liberates 1:8-cineole isopipertenol, 6-methyl-hept-5-en-2-one, and stenusin from its pygidial glands. All these compounds have good surface spreading ability, especially stenusin; thus when they are secreted on the water the insect is able to physically travel along a surface tension gradient. Do any of these components coat the insect with a protective film? This particular allomonal system points out very well the need to consider the possibility of other arthropod secretions functioning in a multitude of roles.



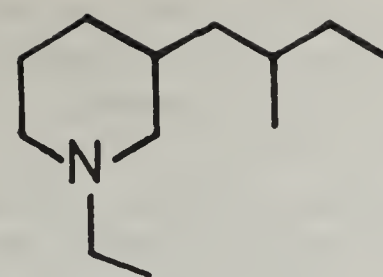
1:8-Cineole



6-CH₃-hept-5-en-2-one



Isopiperitenol



Stenusin

The reaction chamber of the cyanogenic gland of polydesmoid millipedes is shaped somewhat like a Florence flask (Fig. 3). At a initial glance, one could conclude that this enzyme containing chamber is a clever device to prevent mandelonitrile degradation until the moment of defensive action (Eisner and Eisner 1965, Eisner et al. 1963a). However, this cyanogenic apparatus has also some other very subtle morphological and chemical designs that contribute to its physical functionality. The external pore (orifice) of the cyanogenic gland is unblocked by opercula or other restrictive structures. The pore leads directly to the enzyme solution of the reaction chamber. This aqueous enzyme solution would seem like an ideal habitat for certain soil microorganism. How might the millipede keep this solution free of intruders? Millipedes like *Oxidus gracilis* and *Pseudopolydesmus* sp. contain easily detectable amounts of phenol and guaiacol in the reaction chamber (Duffey et al. 1976b). These chemicals should have antibiotic properties against many bacteria and fungi; in fact, in the above millipedes only a phenol tolerant species of *Salmonella* was found in the reaction chamber (Duffey and Blum 1976b).

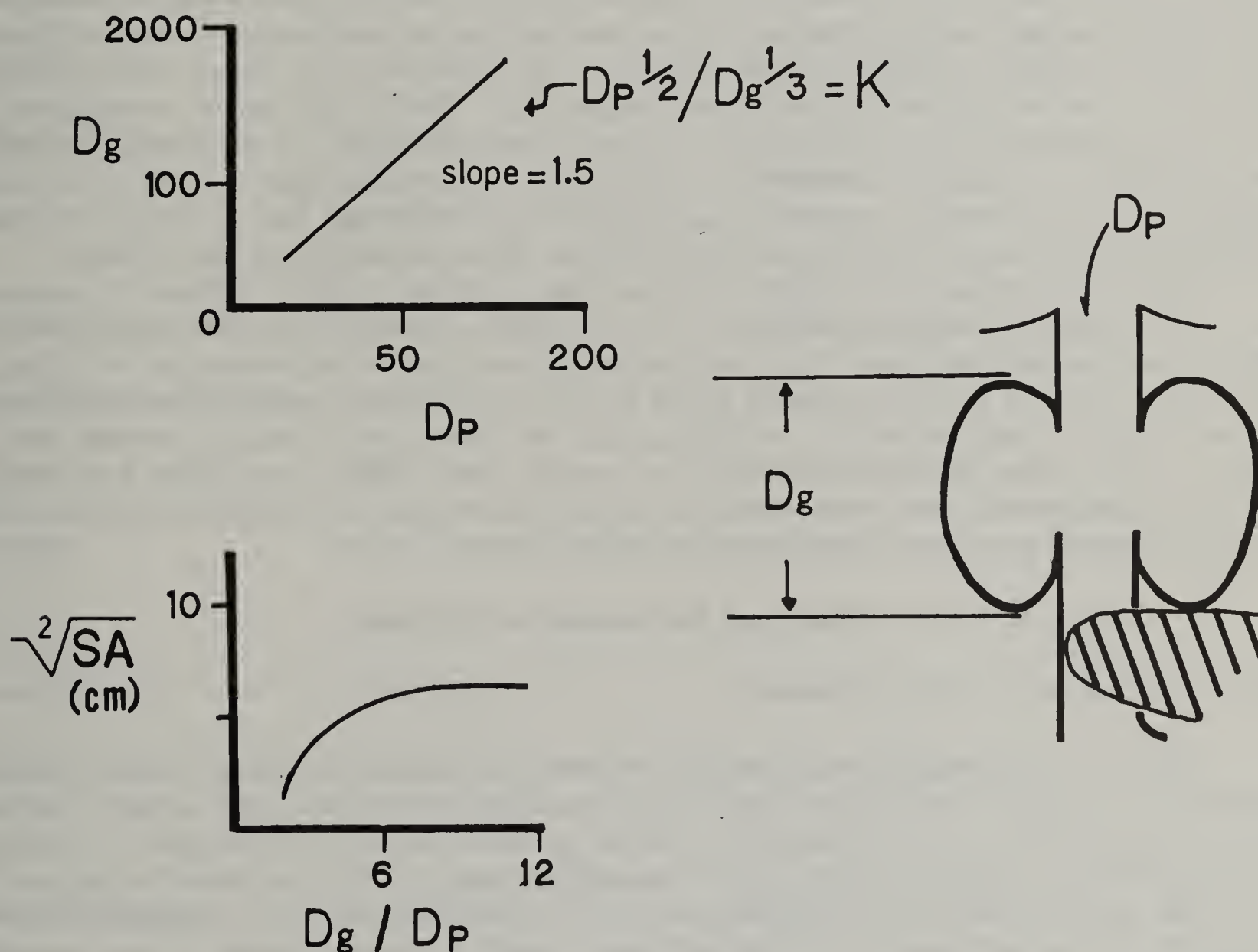


Fig. 3. —Size relationships of the reaction chamber of the cyanogenic gland of polydesmoid millipedes.

Dg = diameter of reaction chamber in micrometers
Dp = diameter of the pore of the reaction chamber in micrometers.
SA = surface area of millipedes in cm²
K = constant

This alone may not be the only mechanism employed for antiseptic activity in the reaction chamber. If one compares the size of the pore opening in a variety of millipedes ranging from 1.5 cm to 9.5 cm in length, it is noted that the diameter of the pore does not increase proportionally with the increase in the size of the animal (surface area; Fig. 3), nor with an increase in the size of the reaction chamber diameter (D_g/D_p). It has been hypothesized (Duffey et al. 1976b) that polydesmoids restrict the size of the cyanogenic pore as they become larger so that they may, not only reduce water loss, but also create a substantial effusion pressure from volatile components like phenol and guaiacol. These chemical inclusions will evaporate to the infinitely diluting environment, this providing a outward vapour pressure which might have the potential to bombard (Brownian motion) small fungal spores, or sol particles containing bacteria away from the pore area. The reduced pore size in large millipedes may represent a morphological adaptation to maintain a sufficiently small pore diameter so as to prevent the loss of an adequate effusion pressure. Also, a reduced pore size in larger millipedes (130 μm instead of a theoretical 333 μm) could limit the entry of mites.

The cyanogenic gland must also be able to effectively eject mandelonitrile to the exterior of the animal such cyanogenesis does not rampantly occur within the reaction chamber. This would result in the loss of the enzyme solution. The evolution of an immiscible moderately viscous cyanogenic material (mandelonitrile) facilitates the hydrodynamically stable ejection of spherical or cylindrical aliquots of mandelonitrile from the storage chamber, through the reaction chamber and hence to the exterior. The dimensions of the cyanogenic reaction chamber (D_p and D_g) in conjunction with the surface tension and viscosity of the cyanogenic liquid enhance the rapid ejection of mandelonitrile to the exterior of the animal without incurring unstable oscillations in the moving aliquot, which would result in the fragmentation of the liquid within the reaction chamber (Duffey and Curzon, unpublished data). It is to be remembered that the expulsion of mandelonitrile from the storage chamber is the result of haemostatic pressure distorting a highly flexible storage sac (Blum and Woodring 1962, Eisner et al. 1963a, Woodring and Blum 1963). This means that a pressure is also placed upon the rigid reaction chamber. If it is assumed that the maximum pressure a millipede can exert while expelling mandelonitrile is limited by the strength of its cuticle, then by physical arguments it can be expected that $D_p^{1/2}$ should vary as $D_g^{1/3}$ (Duffey and Curzon, unpublished data). Indeed, in a analysis of over 100 species of variously sized millipedes, this relationship was found. A very good linear correlation exists between $\ln D_p$ versus $\ln D_g$ with a slope of 1.5 (Fig. 3). This then indicates that the physical process of mandelonitrile liberation has been a factor directing the evolution of the cyanogenic gland, quite apart from the allomonal qualities of the secretion.

From this viewpoint, it would be interesting to know if the evolution of mechanically functional glands has been a central theme in the evolution of other arthropods? In other words, the shape of an eversible gland may not be as important in a size range of arthropods, as would the shape (see Eisner 1970), of bombardier beetle glands squirting hemipteran glands, or glands which produce foams. So much fundamental data are lacking that we cannot even attempt to explain why some beetles utilize similar allomones in pygidial, or sternal glands. Why do millipedes have a bilateral battery of glands while most other arthropods do not? Can we find any correlations between habitat, foes and glandular structure-position, function and chemistry?

Origin and Biochemistry of Allomones

The sequestration of extrinsic allomones

There is a striking chemical parallel between the natural secondary products found in arthropods (see Fig. 1) and those found in bacteria, fungi, plants, and some animals. This parallel raises the question as to whether the natural products found in arthropods are of plant, microorganismal or arthropod origin. Several possibilities exist: a) the chemicals are sequestered from the food source, b) the chemicals are sequestered from the food source and subsequently modified chemically by the arthropod, or by the arthropod's resident microorganisms, c) the chemicals are synthesized by the organism's own metabolic capabilities, or d) the molecules are partially or completely constructed by alimentary, interstitial, or intracellular microorganisms with or without the arthropod's biochemistry. These aspects will be discussed below.

A great variety of plant chemicals is sequestered by phytophagous insects (Table 4). This variety not only encompasses essential factors like amino acids, steroids, salts *et cetera*, but also more peculiar "secondary" components like alkaloids, cardenolides, and terpenes. In many cases the

suspected biological role of these sequestered “secondary” components is a defensive one. Outlined in Table 4 are some examples of sequestered plant compounds and the use to which they are put. Several detailed synopses of this sequestration-defense phenomenon are available (Rothschild 1975, 1972a, 1972b).

The term “sequester” though useful for naming the bodily acquisition of extrinsic chemicals, can be misleading if used indiscriminately. The sequestration of plant chemicals can occur in a multitude of ways. The current use of this term tends not to discriminate between chemicals that reside in the body because of non-specific mechanisms and those that accumulate because of specific or directed processes. The Monarch butterfly *Danaus plexippus* sequesters cardiac glycosides from species of *Asclepias*. This does not appear to be a casual process. The larva accumulates large quantities of cardenolides when fed on *A. curassavica*, and passes these on the adult butterfly where they are deposited in considerable concentrations in the abdomen and wings especially, as well as in other body regions (Brower and Glazier 1975, Parsons 1965). Similarly, some papilionid butterfly larvae are able to sequester aristolochic acids from species of *Aristolochia*, and pass these chemicals on to the adult butterflies. These acids are also accumulated in various portions of the body (vonEuw et al. 1968, Rothschild et al. 1970b, 1972). Another milkweed feeder, the large milkweed bug *Oncopeltus fasciatus* sequesters large quantities of cardenolides in its dorsolateral gland fluid (Duffey and Scudder 1974). The important feature is that in all the above cases the sequestered chemicals are deposited in some regions of the body at concentrations well above those that could be realized

Table 4.—Some plant chemicals sequestered by insects

CHEMICAL	INSECT TYPE	USE
Mustard oils	butterflies ¹	defense
Aristolochic acids	butterflies ²	defense
Cardenolides	butterflies ³	defense
	true bugs ⁴	defense
	grasshopper ⁵	defense
	moths ⁶	defense
Pyrrolizidine alkaloids	moths ¹	defense, communication
Amaryllidaceous alkaloids	moths ⁸	defense
Terpenes	flies ⁹	defense
Hypericin	beetle ^{1 0}	defense
Cycasin	moth ^{1 1}	defense, detoxication product
Norsesquiterpene	grasshopper ^{1 2}	defense
Carotenes	butterflies ^{1 3}	coloration-defense
Flavonoids	butterflies ^{1 4}	coloration
Chloro-insecticides	grasshopper ^{1 5}	defense
	ant ^{1 6}	defense

¹ Aplin et al., 1975; Rothschild, 1972a; ² vonEuw et al., 1968; Rothschild et al., 1970b, 1972; ³ Brower, 1970; Parsons, 1965; Rothschild et al., 1975; ⁴ Rothschild, 1972a; Rothschild et al., 1970a; Scudder and Duffey, 1972; ⁵ vonEuw et al., 1967; ⁶ Rothschild et al., 1973; ⁷ Aplin et al., 1968; Edgar et al., 1973; Meinwald et al., 1971; Pliske and Eisner, 1969; Rothschild, 1972a; ⁸ Rothschild, 1972a; ⁹ Eisner et al., 1974; ^{1 0} Rees, 1969; Rothschild, 1972a; ^{1 1} Teas, 1967; ^{1 2} Meinwald et al., 1968a; ^{1 3} Rothschild, 1975; ^{1 4} Morris and Thomson, 1964; Thomson, 1971; ^{1 5} Eisner et al., 1971a; ^{1 6} Cavill and Houghton, 1974.

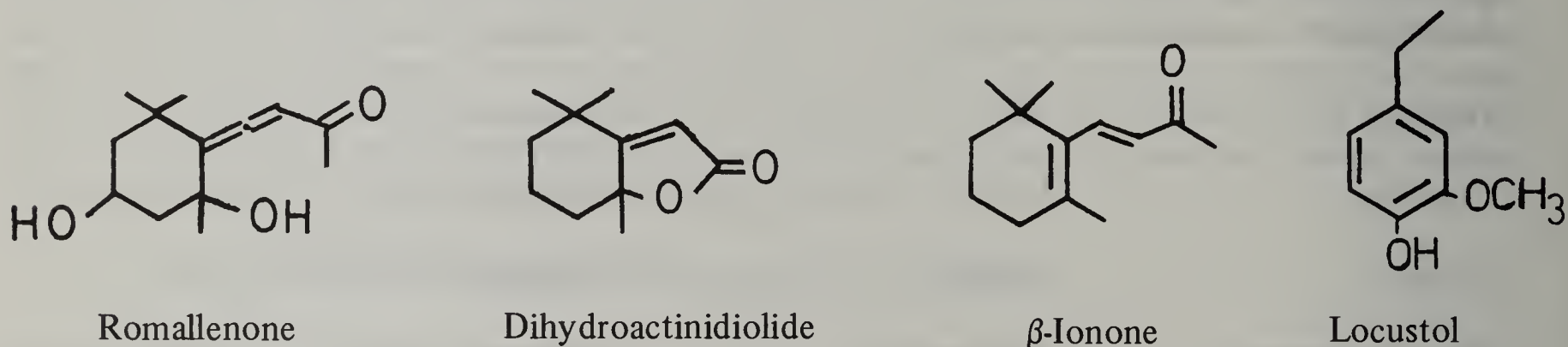
merely by solubility of those chemicals in tissue. This kind of accumulation appears to represent a specific and "purposeful" sequestration against a concentration gradient. It is also clear that in the above larval organisms the sequestered chemicals are predestined for copious storage in the adult tissues. Thus, there is no ambiguity about the source of the chemicals in the adult tissues.

There is ambiguity concerning the source of a variety of supposedly sequestered plant chemicals in certain insects. Although the case is very clear that many lygaeids sequester (take up and accumulate) cardenolides, (vonEuw et al. 1971, Scudder and Duffey 1972) a variety of milkweed feeding insects have been also reported to contain cardenolides (Duffey and Scudder 1972, Rothschild 1972a). Some of these results are ambiguous because no body distributional data was presented to verify that the cardenolides were actually accumulated in a specific tissue or gland. The detected cardenolides could very well have been in the digestive tract. Another possibility is that the cardenolides may have been merely dissolved in body tissues because of their lipophilic properties. This is analogous to cow's milk being flavored by certain plants, DDT accumulating in fatty mammary tissue, or the presence of chlorophenols and dibutyl phthalate in ant secretions (Cavill and Houghton 1974).

This could be the case with the species of *Pieris* studied by Aplin et al. (1975). These authors report, with qualitative data on extracts of whole eggs, larvae, and adults, that allyliosthiocyanate is sequestered from cabbage by the larvae and passed on to the adult butterflies. However, these observations are ambiguous for several reasons. It was not shown that the meconium was not responsible for the carry over. It was not demonstrated that this sequestration process represented a directed accumulation of allyliosthiocyanate. It is equally possible that the amounts of this mustard oil present in the adult butterfly represented the amount that was soluble in the fat body or other fatty tissues, for it can be noted that the glycoside sinigrin (much more polar) was not detected in most of their extracts. In this context it would not be surprising to find that a large number of species of phytophagous insects contained low concentrations of solubilized plant products. The ability of the moth *Arctia caja* to sequester both pyrrolizine alkaloids and cardenolides (Rothschild and Aplin 1971) may reflect this solubilization.

Yet, the fortuitous absorption (sequestration) of small quantities of plant chemicals may be a very important factor in the field, for it could give rise to large regional differences in the flavor or acceptability of prey which have feed on a variety of hosts. Does the dissolution of these plant products in the fat body represent a detoxication mechanism? Is there anything peculiar about arthropods that do not sequester or become contaminated by chemicals in their food?

Some arthropod allomones appears as if they might originate from a combination plant and arthropod metabolism, and perhaps even a contribution from microorganismal metabolism.



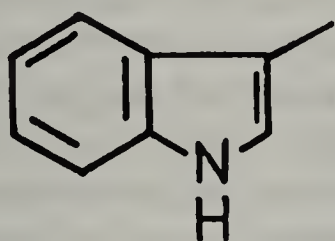
Meinwald et al. (1968b) suggested that the norsesquiterpenoid romallenone found in the grasshopper *Romalea microptera* originates by the ingestion and metabolism of plant xanthophylls. But, perhaps the plant carries out this oxidation since similar compounds are known to arise during "fermentation" of tea and tobacco (Aasen et al. 1972, Sanderson 1972), in which β -ionone derivatives are formed from carotenes and xanthophylls. However, these abscissic acid-like compounds also occur in a free state in plants (Stuart and Woo-Ming 1975, Taylor and Burden 1972), so that this insect might be acquiring a number of chemicals that could provide the nucleus for the formation of romallenone. It is interesting to note that the supracaudal gland of the fox *Vulpes vulpes* produces a number of norsesquiterpene derivatives of which one is dihydroactinidiolide (Albone 1975, Albone and Perry 1976).

A pheromone recently identified in the frass of the locust *Locusta migratoria migratorioides* (Nolte et al. 1973) bears a striking resemblance to the coniferyl derivatives of plants. Those authors suggest the possibility that the insect degrades plant phenolics to produce this pheromone.

The modern use of insecticides may have had its impact even on the defensive secretions of arthropods. Eisner et al. (1971a) reported the existence of 2, 5-dichlorophenol in the defensive fluid of the eastern lubber grasshopper *Romalea microptera*. They suggested that this chemical arose from metabolism of chlorinated insecticides by plants. A recent study by Berger (1976) has shown that this grasshopper is unable to incorporate Na^{36}Cl into 2, 5-dichlorophenol, and concluded that the grasshopper requires an exogenous source of this material. There are many means by which this exogenous source could arise. 2, 4-Dichlorophenol has been identified as a natural product of soil fungi (Ando and Kato 1970). Menzie (1972) reviews the derivation of many chlorinated phenols from biodegradation of insecticides such as DDT and α -BHC. The presence of 2, 5-dichlorophenol in *R. microptera* may be the result of previously extensive metabolism of insecticides by microorganisms and plants, and by photo-oxidation (Matsumura et al. 1972). The co-occurrence of two chlorophenols (di- and trichloroanisole) and dibutyl phthalate in the secretion of the ant *Iridomyrmex humilis* (Cavill and Houghton 1974) is strongly suggestive of environmental contaminants as sources.

Interestingly, 2, 6-dichlorophenol has been identified as one of the pheromones of two species of ticks, *Rhipicephalus* spp. (Wood et al. 1976). Biosynthetic studies employing Na^{36}Cl as a precursor have shown that the ^{36}Cl is incorporated into 2, 6-dichlorophenol by the ticks *Amblyomma americanum* and *A. maculatum*. These divergent results, grasshopper versus tick, demonstrate the need to carefully assess the origin of defensive secretions to avoid ambiguity.

The cantharid beetle *Chauliognathus lecontei* contains a polyacetylenic acid, dihydromatricaria acid, the origin of which is unknown (Meinwald et al. 1968b). It is possible this chemical is derived by the insect feeding upon composites or umbellifers. If, on the other hand, this chemical is produced by the beetle, it would be interesting to know if it arises *via* the oxidation of fatty acids like linoleic or oleic acids (Bohlmann et al. 1973, Geissman and Crout 1969). A similar situation exists with the presence of skatole in a lacewing *Chrysopa oculata* (Blum et al. 1973b). It is not known if this insect acquires skatole from microorganismal activity in the environment *via* their own metabolism of tryptophan, or from the metabolism of symbiotic micro-organisms. There are many other examples of ambiguous origins of arthropod allomones, which provide the opportunity for interesting problems on the sequestration of allomones from plants or microorganisms, or on the comparative biochemistry of *de novo* biosynthesis.



Skatole



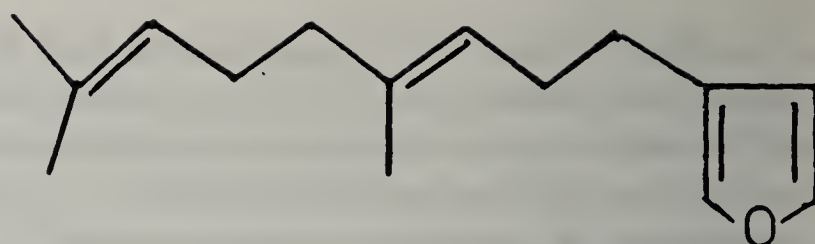
Dihydromatricaria acid

Despite the similar or identical chemical nature of plant and arthropod allomones, some of these arthropod defenses are not of plant origin, because they are produced regardless of the nature of the food. It is therefore logical to ask if the arthropod produces these chemicals *via* biosynthetic pathways that are similar to those of microorganisms, fungi, or plants. Actually, there are few radiolabeled biochemical studies that clearly implicate the arthropod as an autonomous biosynthetic organism, and fewer that elucidate the biochemical pathways employed by arthropods in any detail.

In one of the first investigations to determine the origin of insect defensive secretions (Gordon et al. 1963), the biosynthesis of the scent constituents of the pentatomid bug *Nezara viridula* was studied. They found that acetate-1- ^{14}C was incorporated with low efficiency into hex-2-enal, dec-2-enal, and *n*-tridecane. They concluded that the animal makes its own scent components from acetate. Although this experiment partially establishes the biochemical autonomy of the insect it does not depict the pathway involved and ascribes no tissue of origin. These results are ambiguous because it is possible that a fatty acid might be made first and then broken down to form hex-2-enal. The incorporation of linolenic acid- ^{14}C into this aldehyde in the presence of O_2 has been documented in plants like *Ginkgo* (Hatanaka et al. 1976, Major and Thomas 1972, Major et al. 1972).



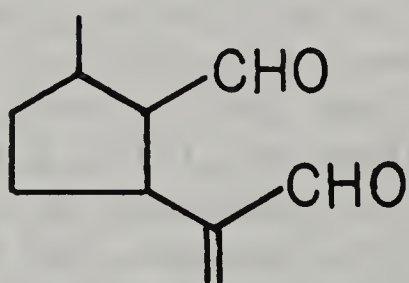
trans-2-Hex-2-enal



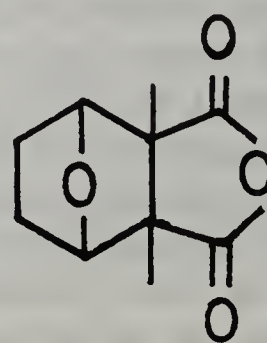
Dendrolasin

Dendrolasin

A furanoterpenoid, dendrolasin, is a component of the mandibular gland defenses of the ant *Lasius fuliginosus* (Bernardi et al. 1967, Quilico et al. 1957). Labelling studies (Waldner et al. 1969) with acetate-1- ^{14}C , mevalonate-2- ^{14}C , and glucose- ^{14}C showed that the first two precursors were incorporated into dendrolasin according to theory (refer to Goodwin 1971, Pridham 1967), into the whole molecule. Degradations of the ^{14}C -product confirmed this. Unfortunately, other terpene derivatives were not administered to test the hypothesis that the animal's pathway is identical to that of the plants. These experiments did not account for the tissue of origin.



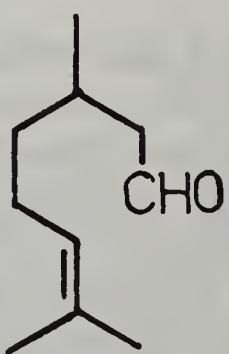
Anisomorphal



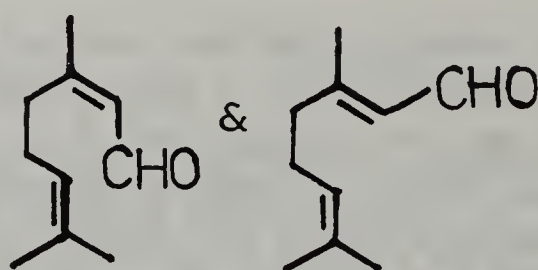
Cantharidin

A similar study by Meinwald et al. (1966a) showed that the monoterpene, anisomorphal, of the phasmid *Anisomorpha buprestoides* was synthesized by that insect from acetate-1- ^{14}C , acetate-2- ^{14}C and mevalonate-2- ^{14}C . Degradation of anisomorph were not undertaken to determine the position of the label. This experiment did not account for the tissue of origin. Also, citral and citronellal produced by the mandibular glands of the ant *Acanthomyops claviger* have been shown to arise from acetate-1 and -2- ^{14}C , and mevalonate-2- ^{14}C (Happ and Meinwald 1965). Again, this study did not indicate where the chemicals were manufactured.

The vesicant, cantharidin, produced by the meloid beetle *Lytta vesicatoria* arises from acetate-1- ^{14}C and mevalonate-2- ^{14}C (Schlatter et al. 1968). Their data derived from partial degradation of cantharidin- ^{14}C suggest a head to head condensation of two isoprene units.



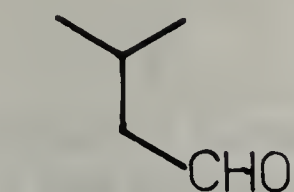
Citronellal



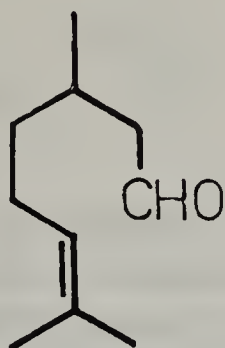
Citral

A recent report on the terpenoid composition of the defensive secretions of several staphylinid beetles, etc., *Eulissus orthodoxus* (Bellas et al. 1974), showed the presence of four chemicals suggestive of the biochemical pathway leading to the production of actinidine. Dolichoderine ants also produce iridoidal monoterpenes as well as acyclic monoterpenes such as citronellal. These ant terpenes have the appropriate functional groups and stereochemistry to be intermediates in a feasible

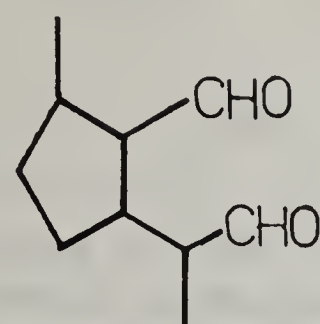
biosynthetic pathway (for details see Cavill and Clark 1971, Weatherston and Percy 1970). Isovaleraldehyde has been shown to be produced from L-leucine- ^{14}C in tomatoes (Yu et al. 1968) and thus the chemical in beetles may not be biogenetically related to terpenoids.



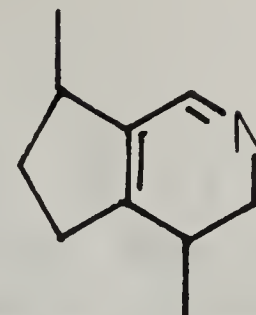
iso-Valeraldehyde



Citronellal



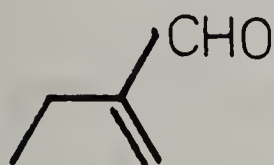
Iridodial



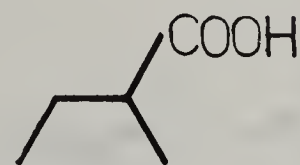
Actinidine

Most of the above isotopic experiments have been based on the injection or feeding of precursors, followed by somewhat specific collection of the natural products. Only in a few cases were thorough degradative analyses undertaken to establish that the distribution of the isotope within the isolated compound was according to biosynthetic theory. Because of this, it is difficult to be exact about the mechanism of biosynthesis. Also in many cases, the most basic building blocks were employed as precursors for compounds that are elaborated by a series of biochemical steps. The lack of utilization of radioactive intermediates along the pathway to the end product, makes it more difficult to confirm the existence of a specific biosynthetic pathway. Granted this is easier said than done, it is still a necessity to either test suspected intermediates or prove their existence by isolation before a pathway can be clearly depicted. Another feature of most of the above experiments is that they do not provide any data describing where the biosynthesis might be occurring. They are ambiguous as to whether the gut, fat body, or glandular tissue is responsible for the biosynthesis. To establish this site is a critical factor in ultimately determining whether the arthropod is biochemically autonomous or is dependent to some extent on microorganisms.

The biosynthesis of many defensive chemicals will not always succumb easily to armchair analysis. For example, the cockroaches, *Platyzosteria* spp., produce 2-methylenebutanal (Waterhouse and Wallbank 1967), which looks very much like a terpene. 2-Methylbutyric acid, a compound with the same carbon skeleton, is however synthesized from propionate- ^{14}C and acetate- ^{14}C (via methylmalonate) in the parasitic worm *Ascaris lumbricoides* (Saz and Weil 1960). Does 2-methylenebutanal arise *via* isopentyl pyrophosphate, from acetate-propionate, or from an amino acid? This remains to be determined.

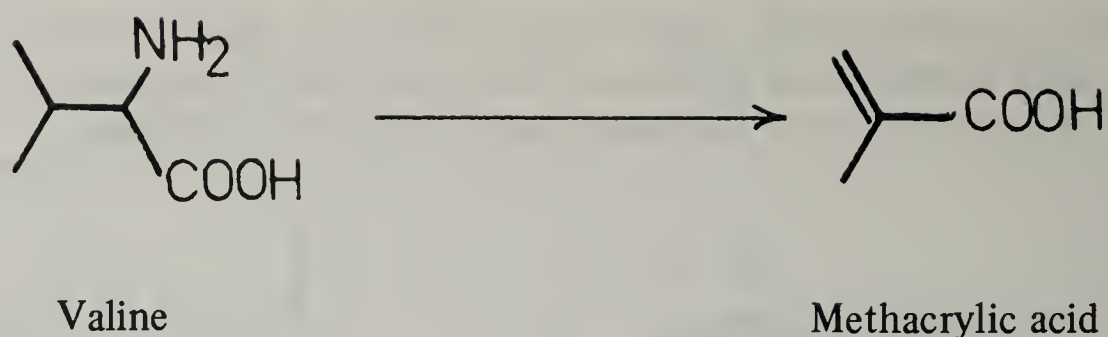


2-Methylenebutanal

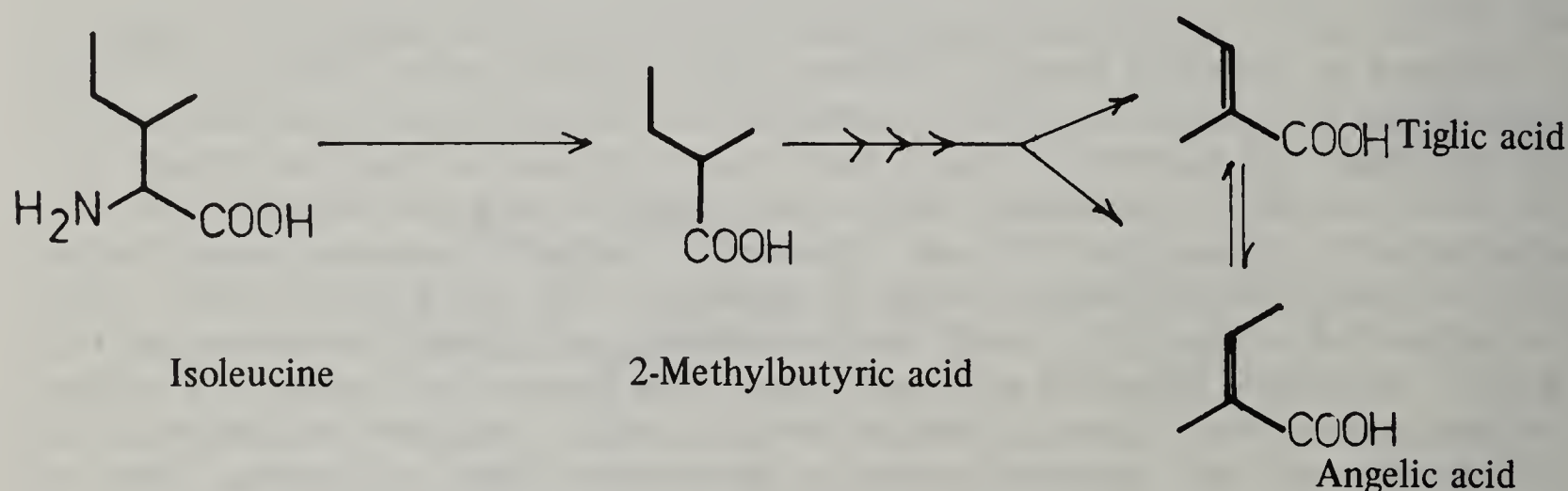


2-Methylbutyric acid

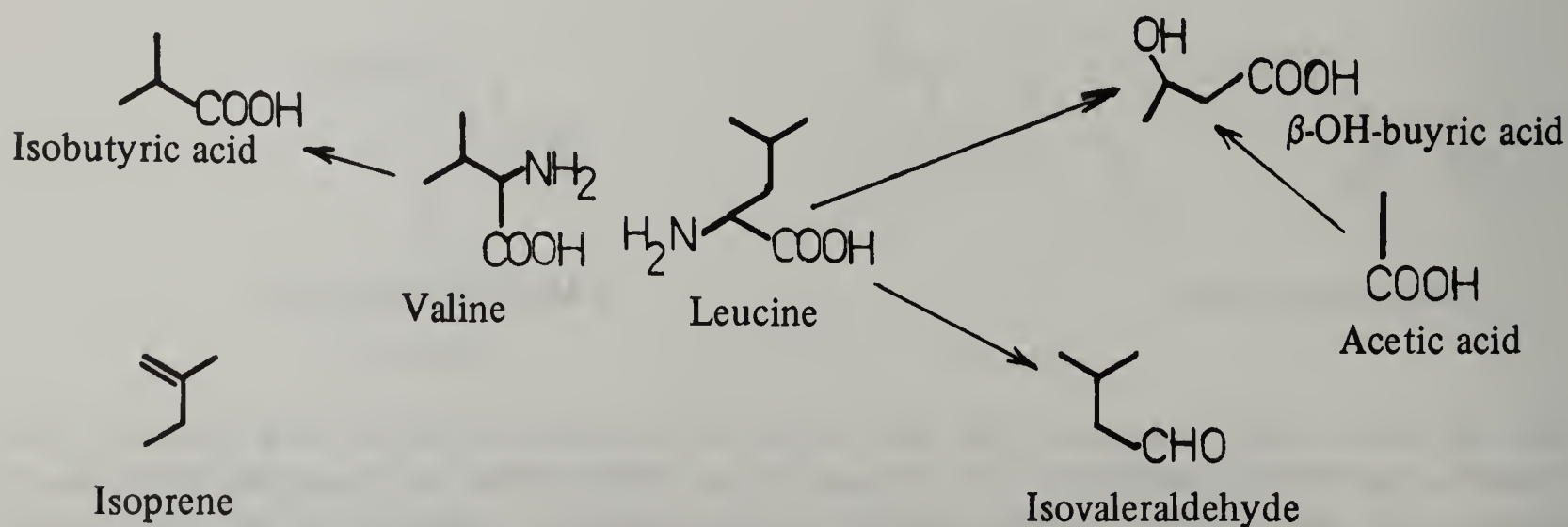
The acrylates, tiglic acid and angelic acid, occur in many beetles (Moore and Wallbank 1968, Schildknecht et al. 1968, Scott et al. 1975, Wheeler et al. 1970). These two chemicals also resemble the isoprene unit. Also methacrylic and ethacrylic acids have been identified in the carabid beetle *Carabus taedatus* (Benn et al. 1973). Preliminary ^{14}C -precursor studies with this beetle showed that D,L-valine-4- ^{14}C was incorporated into methacrylic acid. The position of the label in the acrylate was not determined (Benn et al. 1973).



These results suggest that the beetles synthesize acrylates in an analogous fashion to that of angiosperms. This biosynthesis involves the degradation of isoleucine, *via* 2-methylbutyric acid to either angelic or tiglic acid. The latter two acids are interconvertible by means of an isomerase (Basey and Wooley 1973a, b, Boyle and Fowden 1971, Fowden and Mazelis 1971, Leete 1973). Note that 2-methylbutyric acid arises differently in the plant than in the parasitic worm. 2-Methylbutyric acid is a common defensive chemical in papilionid butterflies (Lopez and Quesnel 1970).

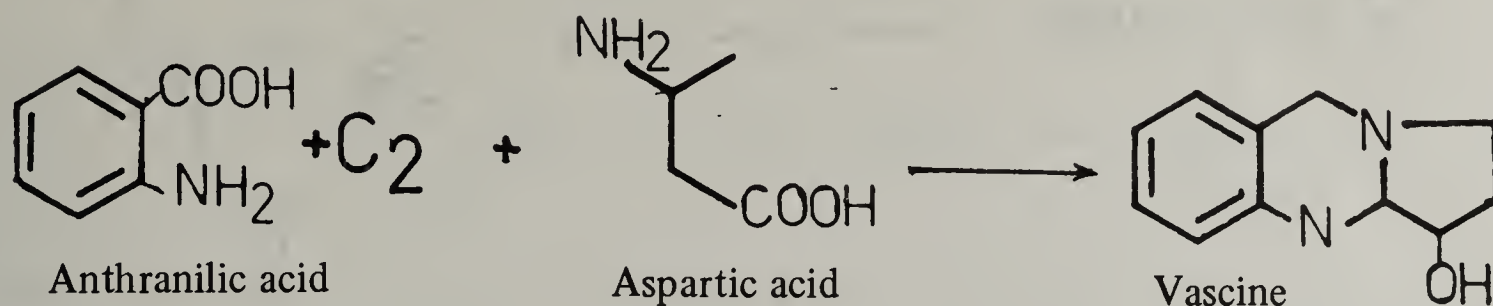


Isobutyric acid has been shown to occur in beetles (e.g., *Broscus cephalotus*, Schildknecht et al. 1968b), the hemipteran *Rhodnius prolixus* (Pattenden and Staddon 1972) and butterflies (e.g., *Papilio aegus*, Eisner et al. 1970, Eisner and Meinwald 1965, Seligman and Doy 1972). In the latter organism β -hydroxybutyric acid occurs alone as an osmetrial secretion of the ultimate larvae. Biosynthetic studies with *P. aegus* (Seligman and Doy 1973) have shown that isobutyric acid arises from valine- ^{14}C , and that β -hydroxybutyric acid arises from acetate- ^{14}C and leucine- ^{14}C . The close resemblance of isobutyric acid to the isoprene unit might make one think it to be derived from mevalonate. Further precursor studies were not done to help elucidate the pathway, but studies were undertaken which showed that the osmetria were metabolically responsible for the formation of these two acids (Seligman and Doy 1973).

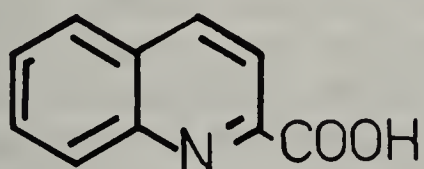


Some biosynthetic schemes are more obvious than those just described. The biogenesis of the quinazolinine (quinazoline) alkaloids, glomerin, from the pill millipede *Glomeris marginata* (Meinwald et al. 1966c) would be expected to involve anthranilic acid. This has been shown by

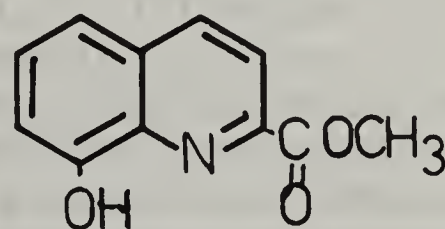
Schildknecht and Wenneis (1967) using anthranilic acid carboxyl- ^{14}C . The formation of the quinazoline alkaloid vascine in plants has been shown to involve anthranilic acid, a C_2 unit (β -carboline position) and an amino acid such as aspartic acid (Liljegren 1971, Luckner 1972).



Likewise, one might expect that the quinoline alkaloid, 8-hydroxy-2-carboxy-quinoline methyl ester produced by the beetle *Ilbybius fenestratus* (Schildknecht 1971) is derived from anthranilic acid and a 3-carbon unit (see Geissman and Crout 1969). An alternative route would involve quinaldic acid, a tryptophan degradation product, which has been detected in the feces of cockroaches (Mullins and Cockran 1973). In fact Schildknecht et al. (1971) have demonstrated that tryptophane- $^{14}\text{COOH}$ is an efficient precursor of methyl 8-hydroxyquinoline-2-carboxylate, with the $^{14}\text{COOH}$ of tryptophane being specifically incorporated into the carboxy-function of the beetle alkaloid.

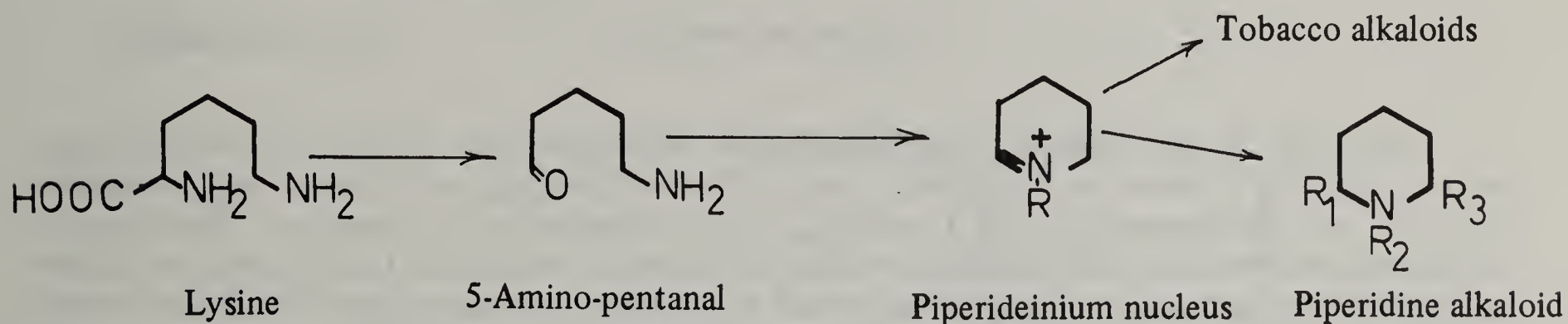


Quinaldic acid

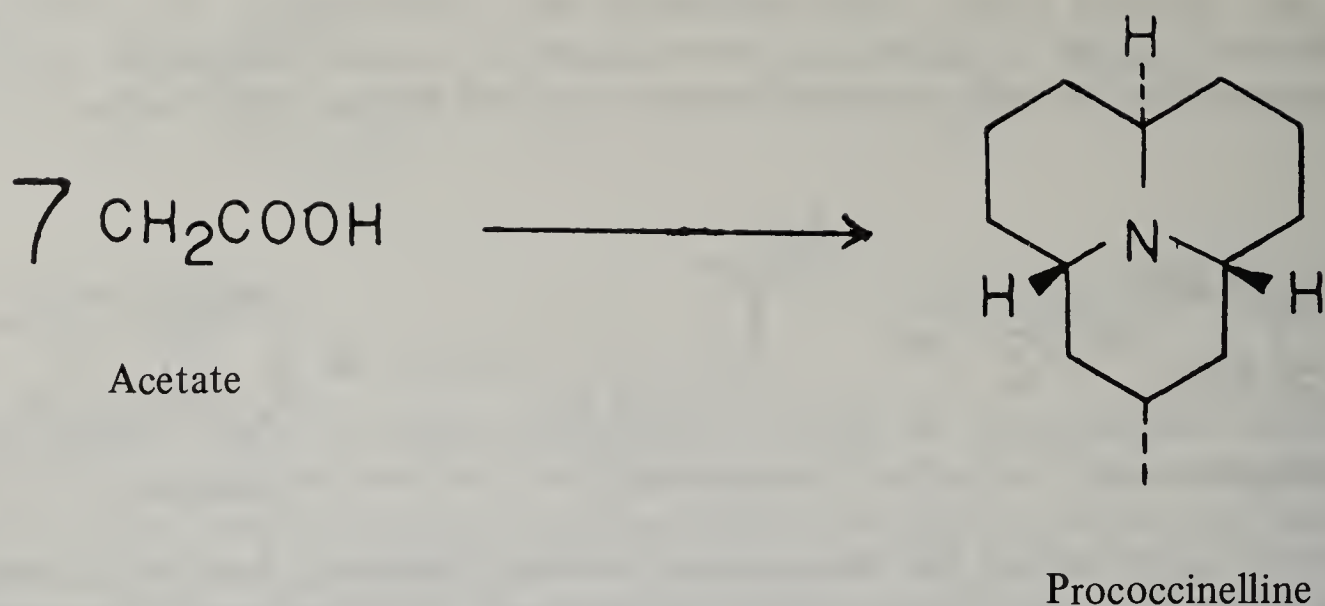


Beetle Quinoline

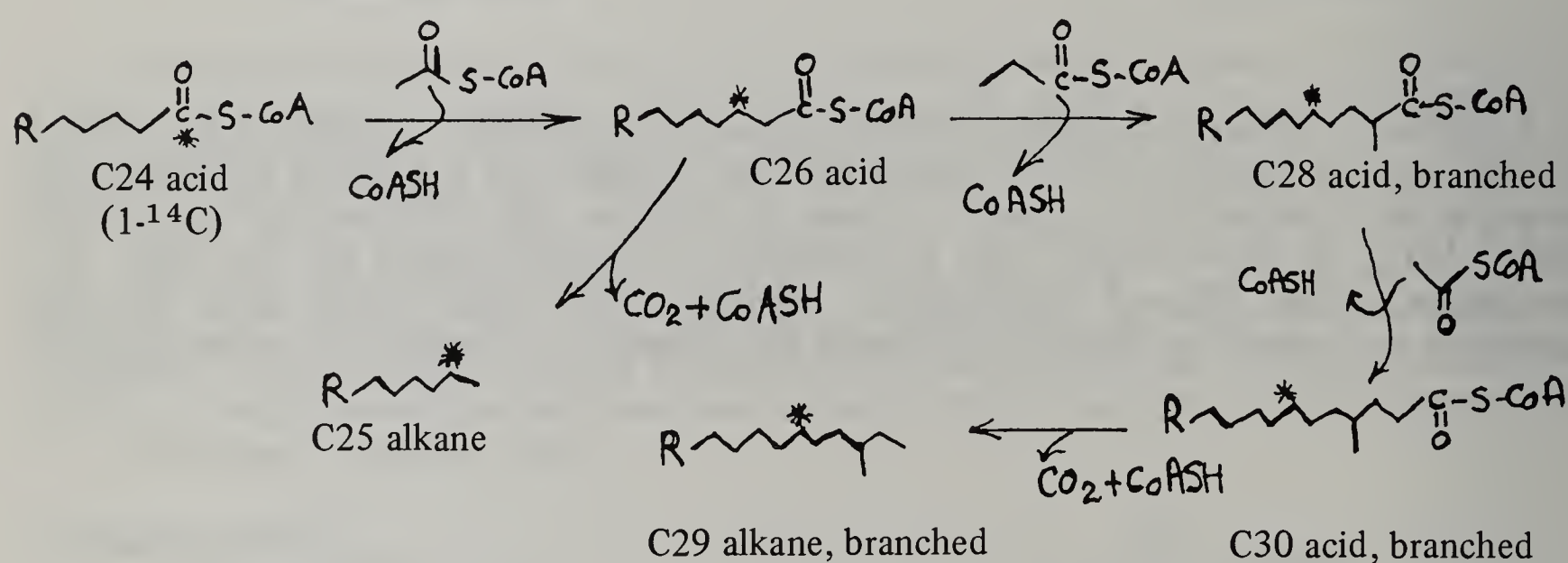
Biosynthetic studies of the dialkylpiperidine alkaloids have not been attempted in the fire ants, *Solenopsis* spp. It is logical however, to suspect that they are elaborated in a fashion analogous to the mechanisms now understood to exist in Solanaceae (Korzan and Gilbertson 1974, Leete and Chedekel 1972). In these plants lysine is converted to 5-amino-pentanal and the latter to a piperideinium nucleus followed by alkylation. Because of the details known about the plant bio-synthetic mechanism, the ants provide a superb opportunity for comparative biochemical studies.



Coccinellid beetles produce a series of complex alkaloids (Pasteels et al. 1973, Tursch et al. 1975) which they harbour in their haemolymph and release by defensive reflex bleeding. These novel alkaloids have been shown to arise via the polyacetate pathway through the condensation of 7 acetate units to form tricyclic structures like prococcinelline (Tursch et al. 1975).



The biosynthesis of alkanes and alkanones in arthropods and plants is poorly understood. It is only partly possible to explain the derivation of chemicals such as *n*-decane, and *trans*-4-oxo-hex-2-en-1-al. It has been known for some time that arthropods are capable of synthesizing their own fatty acids and neutral lipids (alkanes) (Bade 1964, Nelson 1969), but the biosynthetic relationship between them has not been settled, nor has the contribution of blood cells (oenocytes), the fat body and the integument fully understood. Some studies show that insects can absorb dietary alkanes and incorporate them into cuticular lipids. Insects are also able to utilize a variety of alkenoic-1-¹⁴C precursors (C₂-C₂₈) to produce longer chain-length alkanes, alkenes, alkanols, and alkanones (C₂₁ and longer) (Conrad and Jackson 1971, Bloomquist and Jackson 1973). These observations indicate that insects possess an elongation decarboxylation mechanism as described for plants (Kolattukudy 1968, 1970). It was also observed that propionate-1-¹⁴C was incorporated into 3-methyl-branched alkanes which is consistent with an elongation-decarboxylation method (Conrad and Jackson 1971). Lambremont (1972) has reported that insects convert fatty acids-1-¹⁴C into the corresponding alcohols, although it was not determined if this involved a ketonic intermediate.



Apparently in the millipede *Graphidostreptus tumuliporus* the elongation-decarboxylation process exists as a route to long chain cuticular lipids (Oudejans and Zandee 1973). Palmitic acid-1- ^{14}C was incorporated into alk-1-enes (C_{20} - C_{31}), branched and unbranched). This suggests a α -oxidation process for the formation of aldehydes, ketones, and 1-enes. Labelled precursors were not incorporated in the alkanes, suggesting the lack of an alkene reducing enzyme. The alkanes would therefore be of dietary origin. If other arthropods utilize this mechanism of elongation-decarboxylation using either formate, acetate, or propionate, most lipid substances in the cuticle can be accounted for, as well as many defensive chemicals. Coupling these observations with Lambremont's (1972) discovery of the reduction of the carboxyl groups of fats to an alcohol function, the derivation of lipids seems less complex. Thus, if these mechanisms apply to the biosyntheses of short chain fatty acids (C_3 - C_{18}), the biosynthesis of many defensive and pheromonal aldehydes and ketones may be explainable.

A variety of other incomplete but intriguing biosynthetic studies have been carried out which point the way to ideal systems for comparative biochemistry. Schildknecht et al., (1970) have demonstrated that corticosteroids contained in the prothoracic glands of dytiscid water beetles are produced in the beetle from ingested cholesterol- ^{14}C . Are the beetle's degradative pathways similar to those known to occur in vertebrates? The ant *Formica lugubris* has been shown to be able to convert DL-serine-3- ^{14}C into formic acid (Castellani et al. 1969). By what pathway — like bacteria? The african stink ant *Paltothyreus tarsatus* has been shown to produce both dimethyl disulphide and dimethyl trisulphide from L- ^{35}S -methionine, and DL-methionine-methyl- ^{14}C (Crewe and Ross 1975). The production of sulphides occurs in angiosperms, fungi and bacteria, yet not all these organisms accomplish the synthesis in the same manner (Kadota and Ishida 1972, Luckner 1972). By what means does the insect produce both di- and trisulphides? Many of the biosynthetic studies discussed so far point to the diverse opportunities to demonstrate biochemical parallels between arthropods and plants, fungi, and bacteria. Very few studies have been carried out in sufficient depth to permit chemotaxonomic comparisons of biosynthetic pathways.

The most complete study to date on the biosynthesis of a defensive secretion of an arthropod is on the production HCN and benzaldehyde by the millipedes *Oxidus gracilis* (Towers et al. 1972) and *Harpaphe haydeniana* (Duffey et al. 1974). By employing specifically labelled precursors (^3H and ^{14}C), tyrosine, phenylalanine, N-hydroxyphenylalanine, phenylacetaldoxime, 2- α -hydroxy-phenylacetaldoxime, and phenylacetonitrile, it was demonstrated (Fig. 4.) that *H. haydeniana* synthesized HCN and benzaldehyde in manner identical to that known to occur in some angiosperms (Conn 1974). Furthermore, mandelonitrile, phenylacetonitrile, and a glycoside of mandelonitrile were isolated as natural components of this millipede by selected trapping experiments (unpublished data). Isolated cyanogenic glands of *H. haydeniana* were able to synthesize H^{14}CN from phenylalanine-2- ^{14}C , suggesting the biochemical autonomy of the arthropod. Along the same lines the ant *Prorhinotermes simplex* produces 1-nitro-*trans*-1-pentadecene (Vrkoc and Ubik 1974). Does this nitro-alkene arise *via* an oxime intermediate (see Mahadevan 1973)?

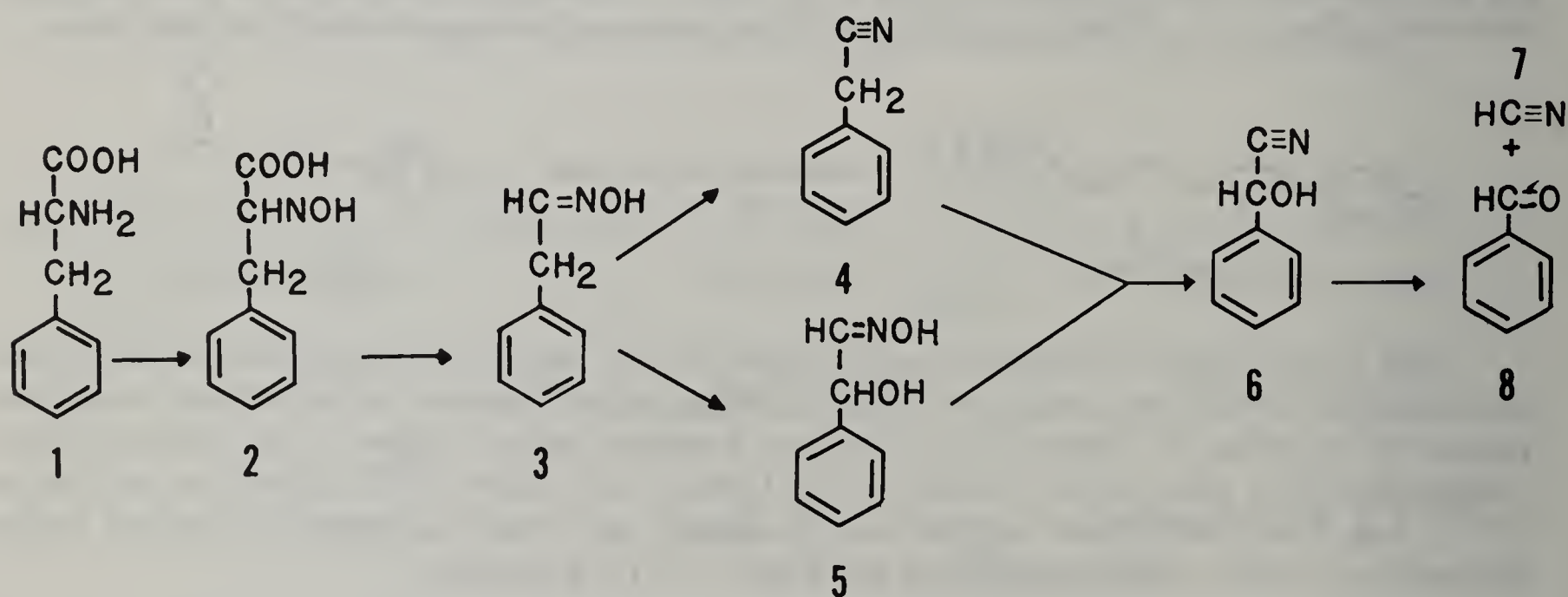


Fig. 4. —The biosynthesis of HCN and benzaldehyde by the millipede *Harpaphe haydeniana*.

¹ Phenylalanine; ² N-Hydroxyphenylalanine; ³ Phenylacetaldoxime; ⁴ Phenylacetonitrile; ⁵ 2-Hydroxyphenylacetaldoxime; ⁶ Mandelonitrile; ⁷ Hydrogen cyanide; ⁸ Benzaldehyde.

Oxidus gracilis, which appears to biosynthesize HCN as does *H. haydeniana* (Towers et al. 1972), also secretes phenol and guaiacol (Blum et al. 1973a). It is known that enterobacteriaceae bacteria transform tyrosine directly into phenol *via* the enzyme tyrosine phenol lyase (Enei et al. 1972). Biosynthetic studies employing tyrosine- ^{14}C and phenol-U- ^{14}C have demonstrated (Duffey and Blum 1976a) that *O. gracilis*, as well as several other polydesmoids, contain the enzyme tyrosine phenol lyase which is capable of transforming tyrosine to phenol (Fig. 5). This enzymatic process is reversible. *In vitro* and *in vivo* studies have also indicated that guaiacol is produced from tyrosine, possible by lyase activity on a metabolite of tyrosine. It also appears that phenol and guaiacol are produced by the subgenital glands of the hemipteran *Legtossus phyllopus* (Aldrich et al. 1976).

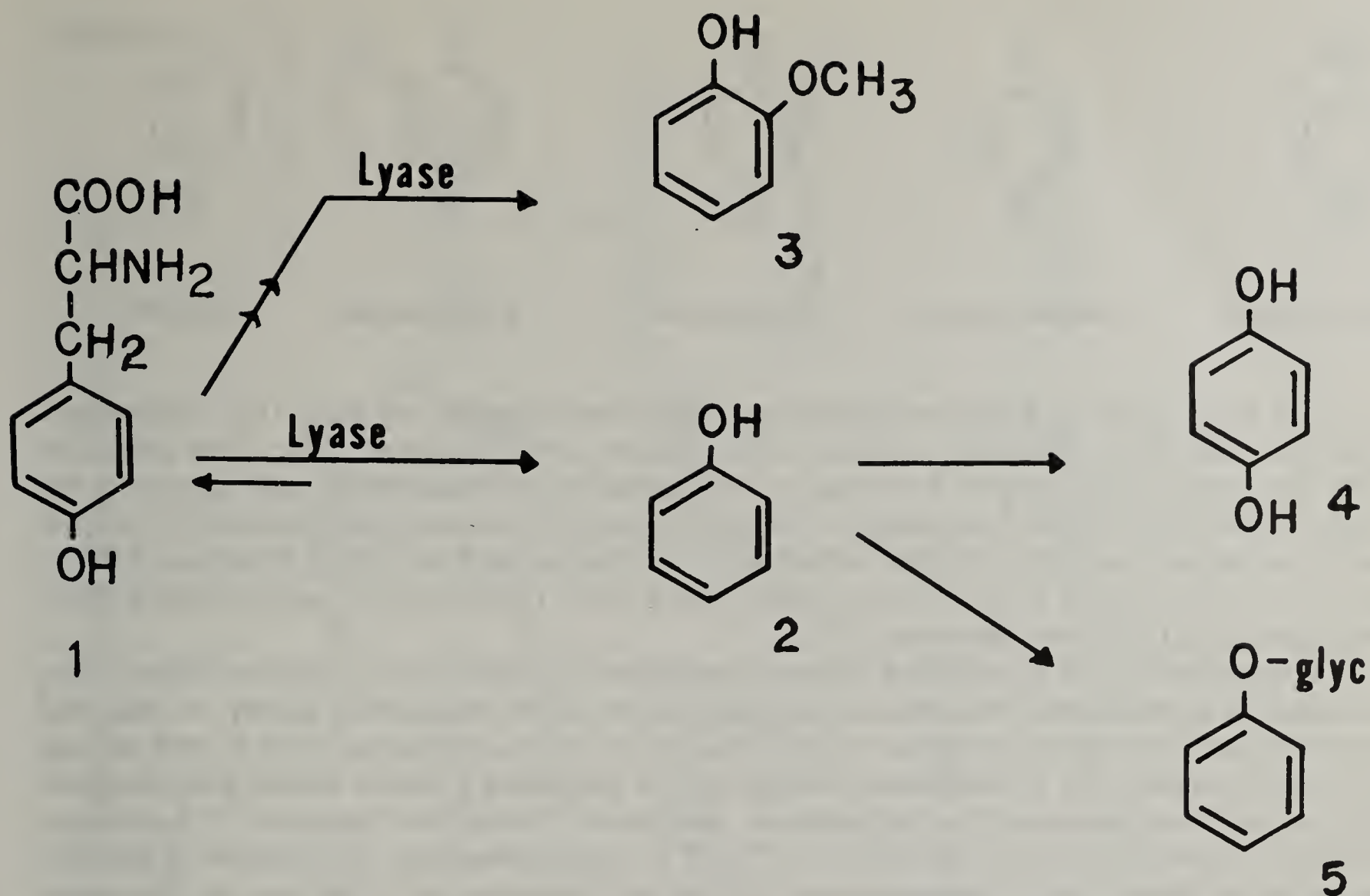


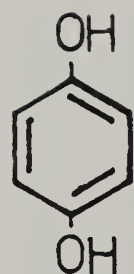
Fig. 5. —The biosynthesis of phenol and guaiacol by polydesmoid millipedes.

¹ Tyrosine; ² Phenol.; ³ Guaiacol; ⁴ Hydroquinone; ⁵ Phenyl glucoside Lyase = Tyrosine phenol lyase (EC.4.1.99.2.).

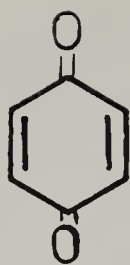
arise from tyrosine phenol lyase activity (Duffey et al. 1976a). This biosynthetic parallel with bacteria suggests that bacteria may in fact be present within the tissues or glands of these arthropods. Hoyt et al. (1971) based on bacterial culture studies, proposed that the sex attractant of the beetle *Costelytra zealandica* was produced from symbiotic bacteria residing in the collateral glands.

However, bacterial culture studies with the above millipedes and the hemipteran indicated that sterilized glands were capable of transforming tyrosine into phenol, and that in *Oxidus gracilis* (unsterilized) only a phenol tolerant species of *Salmonella* could be isolated from the cyanogenic glands (in reaction chamber fluid) (Aldrich et al. 1976, Duffey and Blum 1976a). This bacterium was not able to synthesize guaiacol from phenol. These results suggest that the millipede and hemipteran have independently evolved biosynthetic mechanisms to produce phenol as do bacteria. However, these studies do not rule out the possibility of intracellular symbionts which were anaerobic or unculturable in the experimental conditions used. The bacteria isolated by Hoyt et al. (1971) may only represent phenol tolerant organisms which were contaminants of the lumen of the collateral gland.

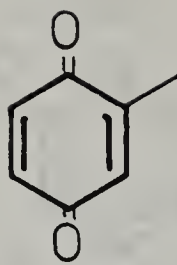
Simple benzoquinones are common defensive agents in beetles, millipedes, earwigs, and a variety of insects. Some elementary biosynthetic studies with the beetle *Eleodes longicollis* have shown that the ring of tyrosine- $\text{U-}^{14}\text{C}$ and of phenylalanine-ring- ^{14}C are incorporated into benzoquinone. The alkyl benzoquinones, toluquinone and ethyl-benzoquinone, were derived from acetate- ^{14}C , malonate- ^{14}C , and propionate- ^{14}C (Meinwald et al. 1966b). These studies did not show the beetles to be wholly responsible for this synthesis, nor in what tissues the chemicals were made. However, very thorough chemical degradations were undertaken to demonstrate that the distribution of the ^{14}C -carbon in the alkyl quinones was consistent with the hypothesis that the beetle employed the polyacetate pathway. The derivation of benzoquinone was conclusively demonstrated to be *via* aromatic metabolism. Yet, these studies are ambiguous because one cannot say for certain that alkyl benzoquinone biosynthesis is occurring *via* intermediates known to exist in fungi, nor by which of a number or possibilities benzoquinone is synthesized. Future studies in arthropod biosyntheses must rely upon the utilization of suspected intermediates rather than just initial precursors.



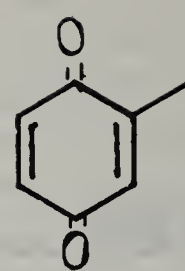
Hydroquinone



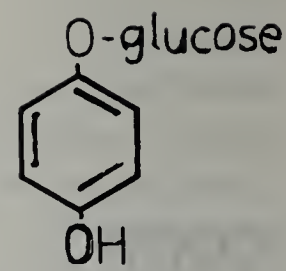
Benzoquinone



Toluquinone



Ethylquinone



Arbutin

The ways by which simple benzoquinones can be biosynthesized are many (for synopses see, Berlin and Barz 1975, Ellis 1974, Luckner 1972, Rudney 1971, Thomson 1971, Toms and Wood 1970, Zenk and Leistner 1968). For instance, benzoquinone and toluquinone could arise from the schemes depicted in Table 5 (a composite of fungal, animal, bacterial, and plant pathways). For more specific details on these pathways refer to Blakely (1972), Berlin and Barz (1975), Clearwater (1975), Enei et al. 1972, French et al. (1976), Grisdale and Towers (1960), Packter and Steward (1967), Terashima et al. (1975), and Thomson (1971).

This multiplicity of hypothetical schemes should lead the reader to two main conclusions. One, it is essential in elucidating biochemical pathways to test at the minimum a variety of suspected precursors, and even more persuasive to give evidence for the mediating enzymes as well as their products. The concept of a biochemical *pathway* can be misleading if one is dealing with metabolic grids as has been evidenced for tryptophane metabolism during the formation of 5-methoxy-tryptamine derivatives (Baxter and Slaytor 1972). Two, chemotaxonomic comparisons of identical compounds in diverse taxa of arthropods are risky because the molecules in question may have arisen by totally different biosynthetic mechanisms.

To recapitulate, the beetle *Eleodes longicollis* (Meinwald et al. 1966b) biosynthesized benzoquinone from the aromatic ring of phenylalanine and tyrosine; acetate was not significantly incorporated into benzoquinone. On the other hand, the alkyl benzoquinones, toluquinone and ethylbenzoquinone, were biosynthesized from acetate, malonate, and propionate according to polyketide pathway theory. There is no reason to conclude from these studies that other arthropods will elaborate their benzoquinones by the above mechanisms. In fact spiroboliform millipedes appear to produce their benzoquinones *via* a different mechanism. Preliminary labelling studies with several species of quinone producing millipedes (*Rhinocricus holomelanus*, *Camabala annulata* and *Narceus annularis*) indicate that only aromatic amino acids can serve as precursors for the biosynthesis of benzoquinone, toluquinone and 2-methoxy-3-methyl-benzoquinone; salts of acetate, malonate, and shikimate were not utilized (Duffey 1974, Duffey and Blum, unpublished data). Thus, toluquinone though chemically identical arises in two different manners when *Eleodes* is compared with diplopods (Fig. 6).

Further studies on this biosynthetic dichotomy are required, though it is tempting to hypothesize that millipedes produce toluquinol from homogentisic acid (Hackmann et al. 1948) as is known to occur in plants (see Ellis 1974). From toluquinol it is possible to derive not only toluquinone, but also 2-methoxy-3-methyl-benzoquinone, and possibly cresols. Homogentisic acid methyl ester is found in some dytiscid water beetles (Schildknecht 1971, 1970), and cresol isomers are found in a variety arthropods (Eisner et al. 1963b, Kluge and Eisner 1971, Schildknecht et al. 1968). However, cresol can very well arise in some animals via the polyketide pathway. The presence of 6-methyl-salicylic acid has been documented many times as a product of fungi (Gatenbeck and Lönnroth 1962, Thomson 1971, Towers 1964). The role of 6-methyl-salicylic acid as an intermediate in the formation of hydroxylated quinones is refuted; however, in some cases it can be hydroxylated to form orsellinic acid, or decarboxylated to form *m*-cresol (Packter 1965, Packter and Steward 1967, Pettersen 1966a, b). *Via* these pathways it is easy to theoretically devise the origin of 2-hydroxy-6-methyl-benzaldehyde (Moore and Brown 1972) which is a defensive chemical in the beetle *Phorocantha semipunctata*.

The biosynthetic origins of dimethyl and trimethyl benzoquinones (Eisner et al. 1974a, Eisner et al. 1971c, Fieser and Ardao 1965), and 2, 3-dimethoxy-benzoquinone (Weatherston and Percy 1969), are open to questions. The co-occurrence of benzoquinones and alkyl-naphthoquinones in the beetle *Agroporis alutacea* (Tschinkel 1972a) raises an interesting biochemical problem. Similar

TABLE V SOME POSSIBLE BIOSYNTHETIC ORIGINS OF TOLUQUINONE AND BENZOQUINONE
IN ARTHROPODS.

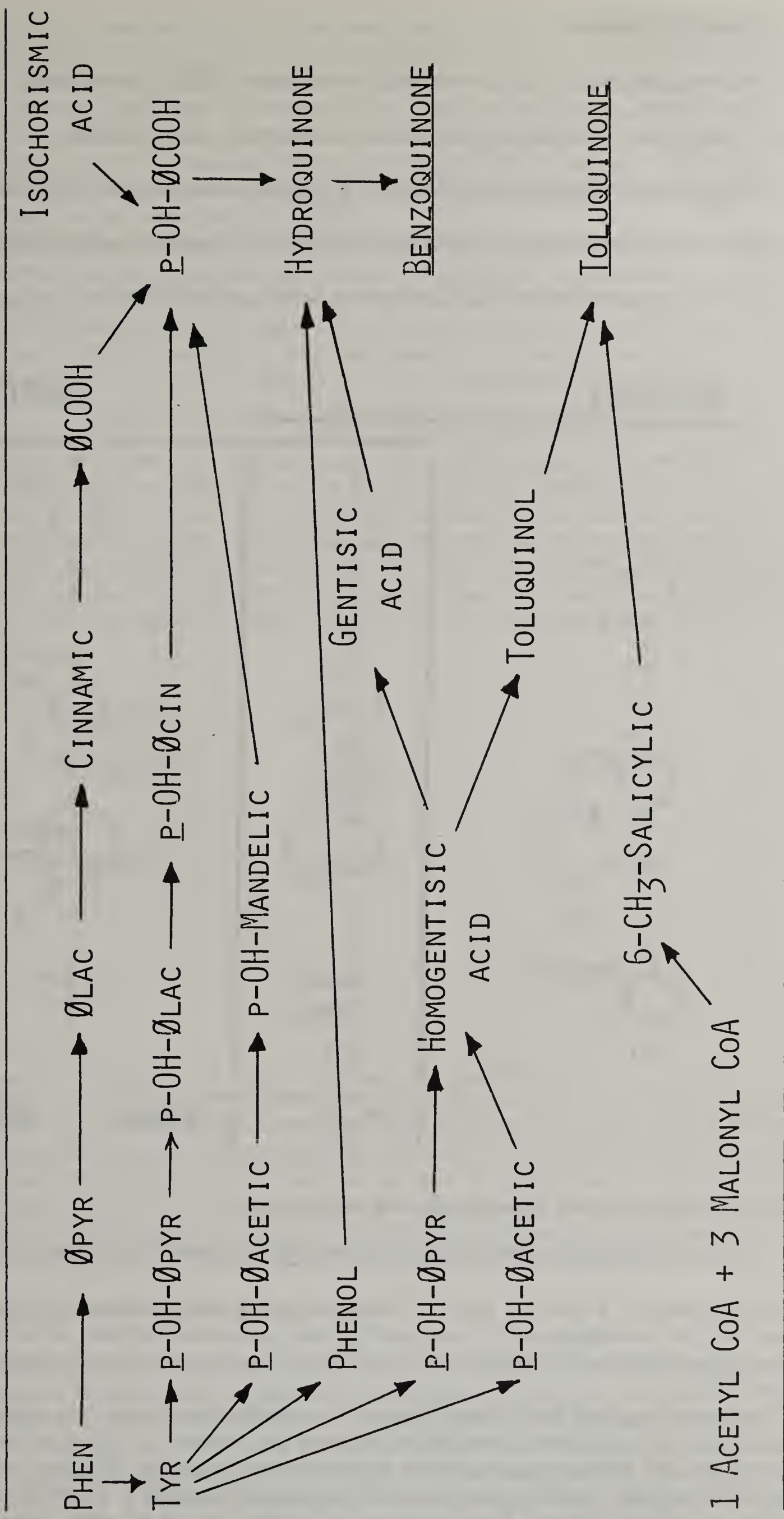


Table 5.—Continued

Phen = phenylalanine; \emptyset pyr = phenylpyruvic acid; \emptyset COOH = benzoic acid;

Tyr = tyrosine; p -OH- \emptyset pyr = p -hydroxy-phenylpyruvic acid; p -OH- \emptyset lac =

p -hydroxy-phenyllactic acid; p -OH- \emptyset cin = p -hydroxy-cinnamic acid; p -OH- \emptyset COOH =

p -hydroxy-benzoic acid; p -OH-Oacetic = p -hydroxy-phenylacetic acid; p -OH-mandelic =

p -hydroxy-mandelic acid; 6-CH₃-salicylic = 6-methyl-salicylic acid.

DIPLOPODA

INSECTA

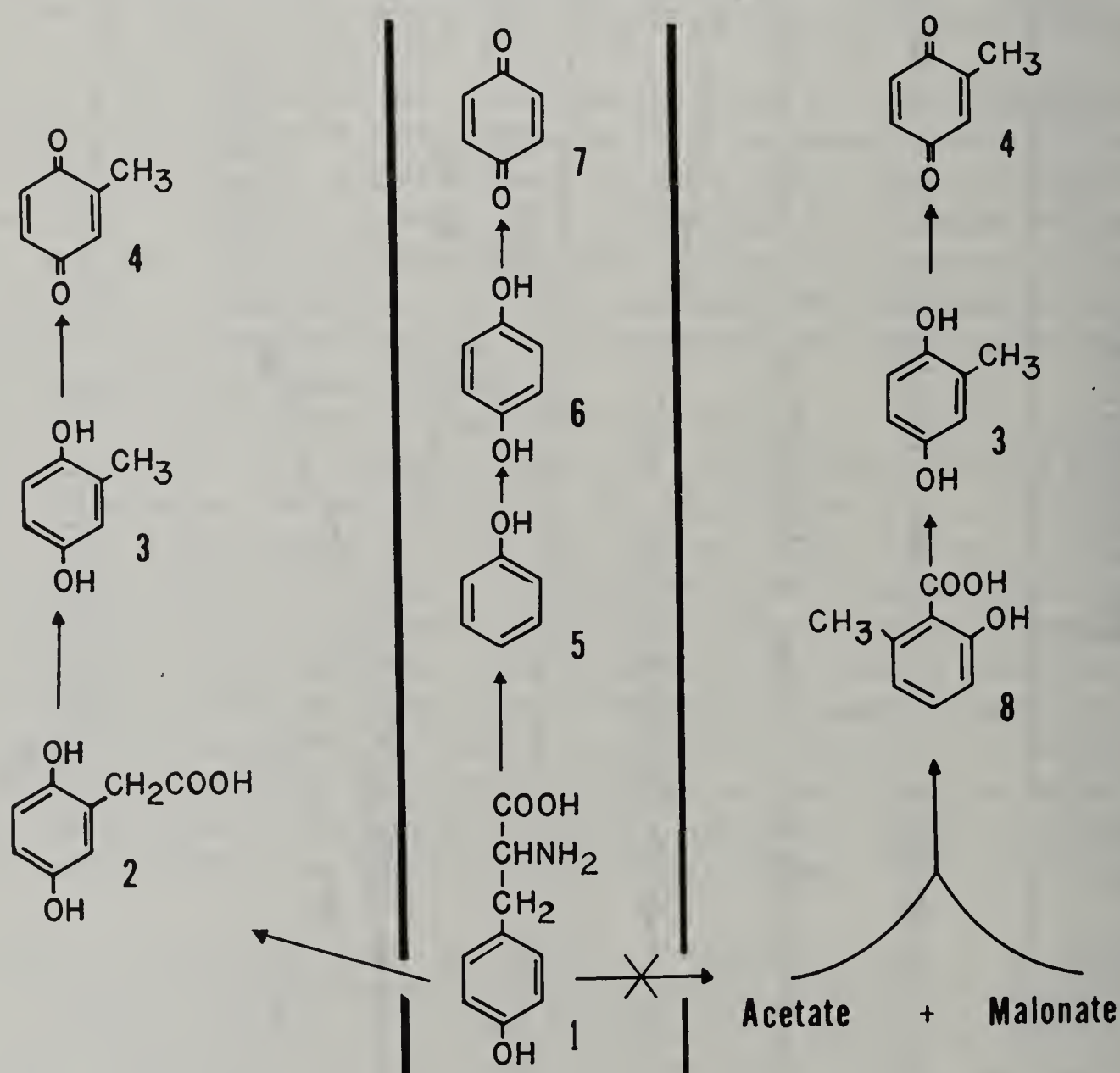


Fig. 6. —The biosyntheses of benzoquinones by arthropods.

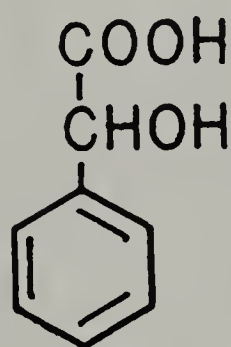
¹ Tyrosine; ² Homogentistic acid; ³ Toluquinol; ⁴ Toluquinone; ⁵ Phenol; ⁶ Hydroquinone; ⁷ Benzoquinone;

naphthoquinones are known to arise, a) from the polyacetate pathway, b) from the shikimate pathway with the contribution of a 3-carbon fragment, a 4-carbon fragment, or an isoprene unit, and c) from the catabolism of tyrosine with the addition of an isoprene unit (Thomson 1971, Zenk and Leistner 1968).

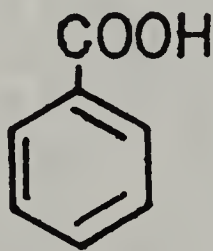
It is interesting that both *Eleodes longicollis* and millipedes produce benzoquinone by aromatic metabolism. In the pear *Pyrus communis* it is known that tyrosine and cinnamic acid were effective precursors for the biosynthesis of arbutin (hydroquinone glycoside) (Grisdale and Towers 1960). Also, the biosynthesis of p -hydroxy-benzoic acid in poplar (Terashima et al. 1975) was shown to arise via shikimic acid phenylalanine *trans*-cinnamic acid *p*-coumaric acid p -hydroxy-benzoic acid. The last

acid can be oxidatively decarboxylated to form benzoquinone (Berlin and Barz 1975), thus it would seem that many plants may utilize the enzyme phenylalanine ammonia lyase (Camm and Towers 1974) as part of the biosynthetic sequence to aromatic acids and hydroquinone derivatives. Clearwater (1975b) has postulated, with very scanty evidence, that the noctuid moth *Mamestra configurata* produces its pheromone phenylethyl alcohol via cinnamic acid. Phenylalanine ammonia lyase has never been detected in animals (Camm and Towers 1974, Towers and Subba Rao 1972). This does not necessarily exclude the possibility of arthropods utilizing this pathway to produce benzoquinone, but there are other likely possibilities.

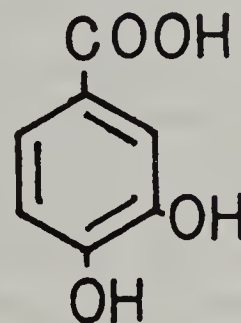
Recently, the biosynthesis of 3, 4-dihydroxy-benzoic acid 4- β -O-D-glycoside in the cockroach *Periplaneta americana* has been partially demonstrated to arise *via* to conversion of tyrosine to 3, 4-dihydroxy-mandelic acid, which is then subsequently converted to the above glycoside (Lake et al. 1975). Therefore, if mandelic acids are employed by insects to produce benzoic, *p*-hydroxy-benzoic and protocatechuic acids, we need not invoke the presence of phenylalanine ammonia lyase (see Andersen 1970, Atkinson et al. 1973, Mills et al. 1967). *p*-Hydroxy-benzoic acid could be formed indirectly from *p*-hydroxy-mandelic acid, which could then be oxidatively decarboxylated to hydroquinone or benzoquinone. Another possibility exists for the formation of benzoquinone. It has been demonstrated that a variety of millipedes can produce phenol directly from tyrosine *via* tyrosine phenol lyase (Duffey and Blum 1976a). In studies with the millipede *Oxidus gracilis* it was found that inhaled phenol-U- 14 C was converted to a product indistinguishable from arbutin. If this is the case it is tempting to speculate that spiroboliform millipedes and beetles also utilize this enzyme to produce phenol which is then hydroxylated to hydroquinone and hence to benzoquinone (Fig. 6). Preliminary experiments with a number of spiroboliform millipedes indicate that tyrosine phenol lyase activity is present and that they are able to convert phenol-U- 14 C into benzoquinone (Duffey and Blum, unpublished data).



Mandelic
acid



Benzoic
acid



Protocatechuic
acid

Many other natural products of arthropods could have a variety of origins (e.g., aromatic aldehydes, alcohols and acids), possibly even in a single organism. The opportunities for thorough comparative biochemical research are immense. In some cases the distinctive advantage of utilizing arthropods for such biosynthetic work is that the isotopic precursors can be injected and the end products often collected in a highly pure natural exudate. The clean up procedure prior to analysis let alone the problem of administration is often the most laborious portion of plant biosynthetic studies. It is strange that arthropods are utilized to such a limited extent when they offer so much.

The role of microorganisms in allomonal biosynthesis?

A complicating factor in the study of the origin of defensive chemicals in arthropods is the ability to distinguish unambiguously between the metabolism of the insect and that of commensal and symbiotic microorganisms. The function of microorganisms in the synthesis of essential amino acids for insects is well documented (Dadd 1973). The occurrence of dimethyl sulphide produced in an apparently bacteria-like manner (Crewe and Ross 1975) in ants, and the presence of tyrosine phenol lyase, considered a bacterial enzyme, as a means of producing phenol in polydesmoid millipedes (Duffey and Blum 1976a) might raise one's suspicions as to the possible contribution of

symbiotic bacteria. To exclude the possibility of metabolic sharing between glandular bacteria and their arthropod host is no simple task.

As previously mentioned, Hoyt et al. (1971) claim that a symbiotic bacterium in the collateral gland of the beetle *Costelytra zealandica* was responsible for the production of phenol. These results are ambiguous for they do not prove that the beetle's sterilized glands have no enzymatic activity capable of producing phenol. A similar situation was encountered in the biosynthesis of phenol and guaiacol by several polydesmoid millipedes, where a species of *Salmonella* could be isolated as a glandular contaminant (capable of producing phenol but not guaiacol from tyrosine, Duffey and Blum 1976a), yet the sterilized gland was *in vitro* capable of producing both phenol and guaiacol from tyrosine. This latter experiment suggests that the millipedes might be autonomous. Yet, these results are still ambiguous for it has not been demonstrated that the glandular tissue does not contain aerobic or anaerobic symbiotic bacteria which were not detected because of the culture techniques employed. In all future studies more sophisticated culturing, biochemical electron-micrographic and techniques should be utilized to achieve more precise answers.

The literature on the production of pheromones by bark beetles *Dendroctonus* sp., *Ips* sp, indicates that host plant chemicals (α - and β -pinene; myrcene) are transformed after ingestion in the digestive tract to sex pheromones and aggregation substances (verbenone and verbenol; ipsdienol, and myrcenol, examples respectively) (Hughes 1975, 1974, Renwick 1973, Renwick et al. 1975). In all these and related studies it is unclear whether the beetle itself and/or the intestinal microorganisms are responsible for the metabolism of the plant substances to pheromones. A number of studies implicate the metabolism of the beetle because of interspecific metabolic differences (fed on same food source) and sexual dimorphism in the ability to produce *trans*-verbenol or ipsdienol (Hughes 1975, 1974, 1973, Renwick et al. 1976).

On the other hand, it is known that many bacteria, like pseudomonads, have the ability to metabolize α - and β -pinene to verbenol *et cetera* (Fonken and Johnson 1972, see Brand et al. 1975). This bacterial phenomenon has let people to postulate that it is gut symbionts which are infact producing the beetles' pheromones (Brand et al. 1975). This suggestion may be appealing, but it is difficult to envisage insect control mechanisms which would permit interspecific metabolic variation as well as sexual dimorphism in pheromone production. Until more convincing evidence is provided on bark beetles demonstrating the presence or absence of gut enzymes, it is reasonable to assume that these gut bacteria may represent forms which are tolerant or able to utilize plant terpenes as sources of carbon. Therefore, their occurrence in the guts of bark beetles may represent a metabolic coincidence as has been suggested for the presence of *Salmonella* in the cyanogenic glands of phenol producing millipedes (Duffey and Blum 1976a). The work of Raisbeck (1975, 1972) indicates that the production of cockroach (*Periplaneta americana*) pheromone is mediated by microsomal oxidases. Obviously, more critical experiments are needed to distinguish between the beetle and bacterial metabolic transformations. At present, the role of symbiotic organisms in the production of allomones or pheromones can not be included or excluded.

The possibility of bacterial contaminants in the defensive glands (e.g., of polydesmoids or beetles) of arthropods introduces the possibility of chemical contaminants in defensive secretions. If this phenomenon is real, great local and geographical variations in defensive quality could arise by varietous bacterial contaminants. The role of bacteria in the anal pockets of the Indian mongoose (Fermentation hypothesis: Gorman 1976) has been suggested as a means by which the animals can acquire distinctive odours, functional in communication. Although the presence of fermentive bacteria in the anal glands affects the quality of the secretions, Albone and Perry (1976) argue that the profiles of volatiles from the glands not constant enough to confer unique odours to given populations. Does anything of a similar nature occur in arthropods?

Detoxication processes

How is it that many arthropods store and liberate allomonal substances with often devastating consequences for the foe, yet themselves remain physiologically unperturbed? Can one assume that during the evolution of many allomonal systems an accompanying evolution of physical and biochemical mechanisms occurred which would stead the organism against the chance of autotoxication? Remold (1963) pointed out that both wholesale bodily spreading and internal contamination by the odiferous secretions of certain hemipterans could result in death for the bearer. The evaporatorium of the scent gland is clearly designed to restrict spreading of the defensive

secretion. A great gap in our knowledge exists as to how the glandular apparatus withstands the toxic effects of the stored secretion. We know virtually nothing about secretory process into the lumina of glandular areas, the permeability of the luminal cuticular lining, or the presence of intimal or bodily (should there be bodily contamination) detoxifying enzymes if leakback from the lumen occurs. Some arthropods appear to employ glycosides of toxic alcohols as a means of avoiding toxicity (Clearwater, 1975a, 1975b; Happ 1968) prior to hydrolyzing the glycoside to an active agent at the lumen-secretory cell interface. Are analogous processes present in glands that secrete anisomorphals (Happ et al. 1966), or a variety of compounds like terpenes, alkaloids, and aliphatic aldehydes and ketones?

How are blood borne allomones like cantharidin (Carrel and Eisner 1974) tolerated by the meloid beetles; or is the concept of vesicant activity even validly extrapolated to arthropods? Might there be haemolymph proteins which bind cantharidin so that it is not physically available to toxify the insect? Both juvenile hormone and ecdysone are known to be bound by haemolymph proteins (Butterworth and Berendes 1974, Chino and Gilbert 1971, Emmerich 1970, Thamer and Karlson 1972); in this fashion they are not available to all tissues bathed by the haemolymph.

Many blood borne substances arise from the arthropod's food. Tobacco feeding insects are known to metabolize ingested nicotine to less toxic chemicals, and as a result in an insect like *Protoparce sexta* the nicotine levels in the haemolymph never reach critical levels. (Schmeltz 1971, Self et al. 1964a, 1964b, Yang and Guthrie 1969). The silkworm *Bombyx mori* detoxifies in the fat body phytoecdysones to physiologically less active compounds (Hikino et al. 1975). The moth *Seiriarctia echo* derives an extremely toxic substance, methylazoxymethanol, (Smith 1966, Yang and Mickelson 1969), by feeding upon species of *Cycas*. The plant contains the β -glycoside, which upon ingestion by the moth, is hydrolyzed to the above alcohol. The moth apparently avoids the toxic effects of this alcohol by converting it to a β -glycoside (Teas 1967). From these examples, it can be seen that insects can evolve elegant means of dealing with foreign toxicants. One also wonders how certain insects like the tiger moths can tolerate pyrrolizidine alkaloids (Aplin et al. 1968), or a variety of insects store prodigious quantities of cardenolides (Brower 1969, vonEuw et al. 1967, Parsons 1965, Scudder and Duffey 1972). However, as a precautionary note, it may not always be unwise to extrapolate physiological responses observed in vertebrates to invertebrates. Cardenolides provide a good example of this type of bias. Cardenolides are generally considered fairly specific inhibitors of Na^+ - K^+ linked ATPase pumps. If an insect were to have uncoupled Na^+ and K^+ pumps, the toxicity of cardenolides might be irrelevant to the insect.

It is known that arthropods are able to detoxify natural and synthetic substances *via* microsomal oxidases (e.g., hydroxylation), the formation of glycosides, glucuronides, and peptides, the formation of sulphate or phosphate esters, and the acylation of NH_2 functions as examples (Agosin and Perry 1974, Binning et al. 1967, Freeland and Janzen 1974, Hitchcock and Smith 1966, Kreiger et al. 1971, Menzie 1972, Raymond et al. 1972, Smith 1962). In contrast, very little is known about how arthropods like cyanogenic millipedes and quinone-phenol producing arthropods detoxify their own allomones that may be inhaled, absorbed through the cuticle, or possibly leak internally from the glands. Cyanogenic zygaenid moths have the ability to convert HCN to SCN (thiocyanate) more proficiently than non-cyanogenic insects (Jones 1972, Jones et al. 1962, Parsons and Rothschild 1964). Also, in the polydesmid millipede *Oxidus gracilis* it has been demonstrated that the majority of H^{14}CN inhaled is converted to S^{14}CN (Duffey and Blum 1976a). It is interesting to note from a comparative biochemical point of view, that both *O. gracilis* and *Harpaphe haydeniana* convert small amounts of H^{14}CN to β -cyanoalanine- ^{14}C and asparagine- ^{14}C , a pathway (Fig. 7) which is characteristic of ^-CN metabolism in legumes (Duffey and Blum 1976, Duffey et al. 1974). Millipedes like *O. gracilis* also face exposure to phenol, and it is known that inhaled phenol is detoxified by conversion to phenyl glycoside, arbutin (Fig. 5), and tyrosine (Duffey and Blum 1976b). Millipedes like *H. haydeniana* also detoxify benzaldehyde by converting it to *p*-hydroxy-benzoic acid (Fig. 7, Duffey and Towers, unpublished data). With the above mechanisms for detoxication of HCN, perhaps one need not invoke (Hall et al. 1971, 1969), the presence of oxidative respiratory bypasses or CN insensitive cytochrome oxidases. If the above studies of the detoxication of an insect's own allomones are any indication of the novel pathways yet to be discovered in arthropods, some interesting discoveries may be in store as to how arthropods biochemically deal with plant allomones.

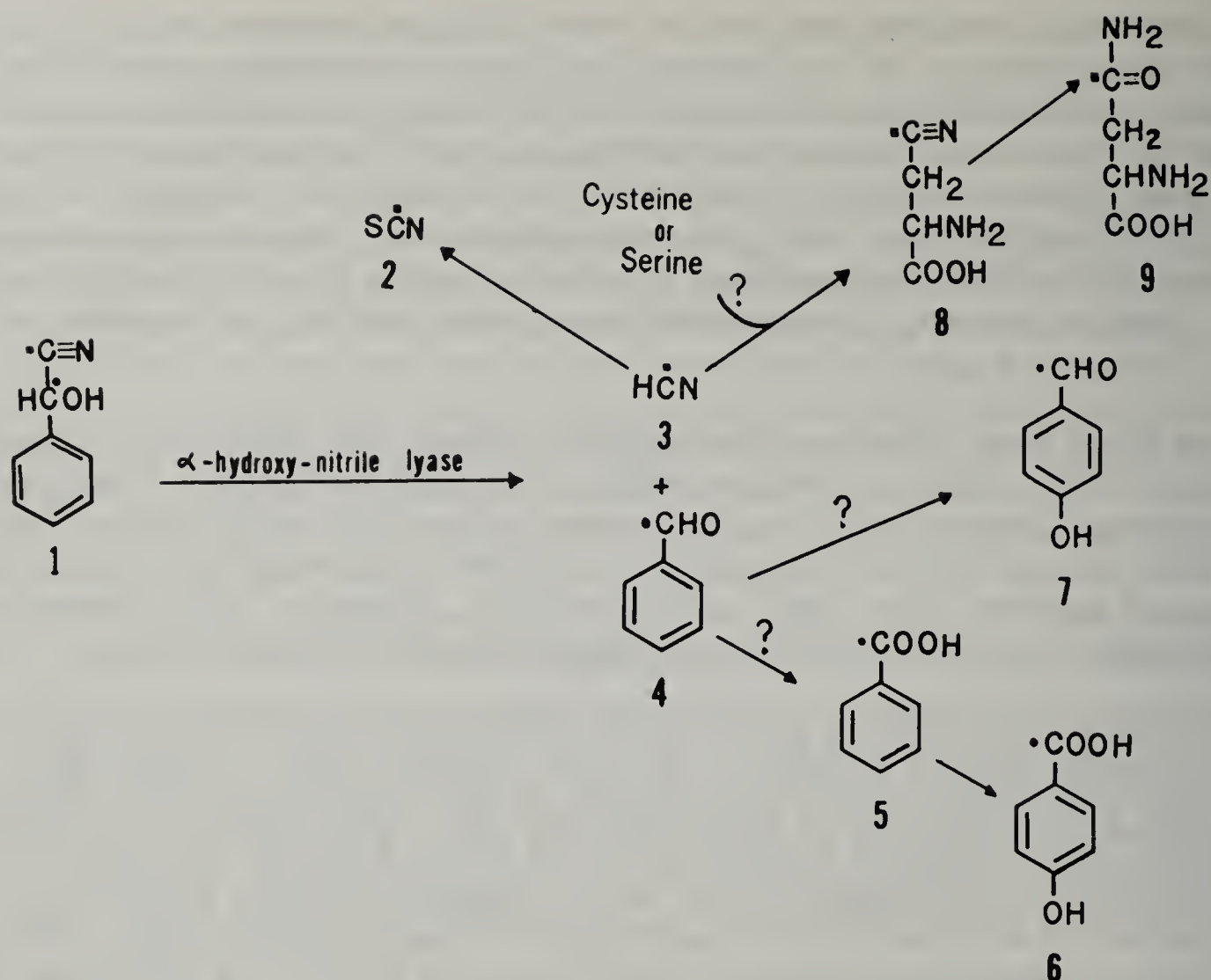


Fig. 7. –The detoxication of HCN and benzaldehyde by polydesmoid millipedes.

¹ Mandelonitrile; ² Thiocyanate; ³ Hydrogen cyanide; ⁴ Benzaldehyde; ⁵ Benzoic acid; ⁶ *p*-Hydroxybenzoic acid; ⁷ *p*-Hydroxybenzaldehyde; ⁸ β -Cyanolalanine; ⁹ Asparagine;

The Process of Sequestration

It has been discussed (physical functions) in a previous section of this article, that defensive compounds could be sequestered from the secretory tissues by the presence of a carrier solvent (*n*-tridencane) which would create a physical sink for other chemicals because of an extremely high partition coefficient towards the carrier. The mass flow of soya bean oil into the post-pharyngeal glands of the ant *Atta cephalotes* (Peregrine et al. 1972) may be just this type of process.

Another means of sequestering allomones in the lumen of a gland is by employing a concentration process based on Gibbs phase rule (see Maron and Prutton 1968). This is by no means a fantastic suggestion, since experiments on the sequestration of cardenolides into the dorsolateral glands of the large milkweed bug *Oncopeltus fasciatus* demonstrate that uptake is a physical process (Duffey and Blum, unpublished data). If this bug feeds for 5 days upon a seed that has been impregnated with either 40 or up to 10,000 picomoles of ouabain-³H, the uptake into the glandular fluid is proportional to the concentration of ouabain-³H in the seed ($\log_{10} \text{ uptake} = \log K + n \log_{10} \text{ concentration}$, where $k = \text{constant}$ and $n = \text{slope} = 1$). Likewise, if ouabain-³H is injected into the haemolymph at concentrations ranging from 4×10^{-7} to $4 \times 4 \times 10^{-3}$ Moles/Lit, of haemolymph, the uptake into the gland fluid is again proportional to the amount injected. The data in Fig. 8 demonstrate that within three hours after injection of the above amounts of ouabain-³H, at time too short for all the cardenolide-³H to be sequestered from the haemolymph, significant gland fluid to haemolymph ratios are obtained ($\log F/H$ vs. amt. injected). These experiments have also demonstrated that at concentrations below 4×10^{-6} Mole/Lit. of haemolymph sequestration does not occur (F/H ratio = 1).

This critical concentration for sequestration to begin and the double log relationship of uptake versus concentration is not characteristic of enzymatic or metabolic energy dependent processes. The only mechanism for sequestration that can account for the data obtained to date is that *Oncopeltus fasciatus* employs a physical process akin to phase formation. Indeed, phase microscopic examination of the dorso-lateral gland fluid demonstrates the presence of an emulsion, whose disperse phase size

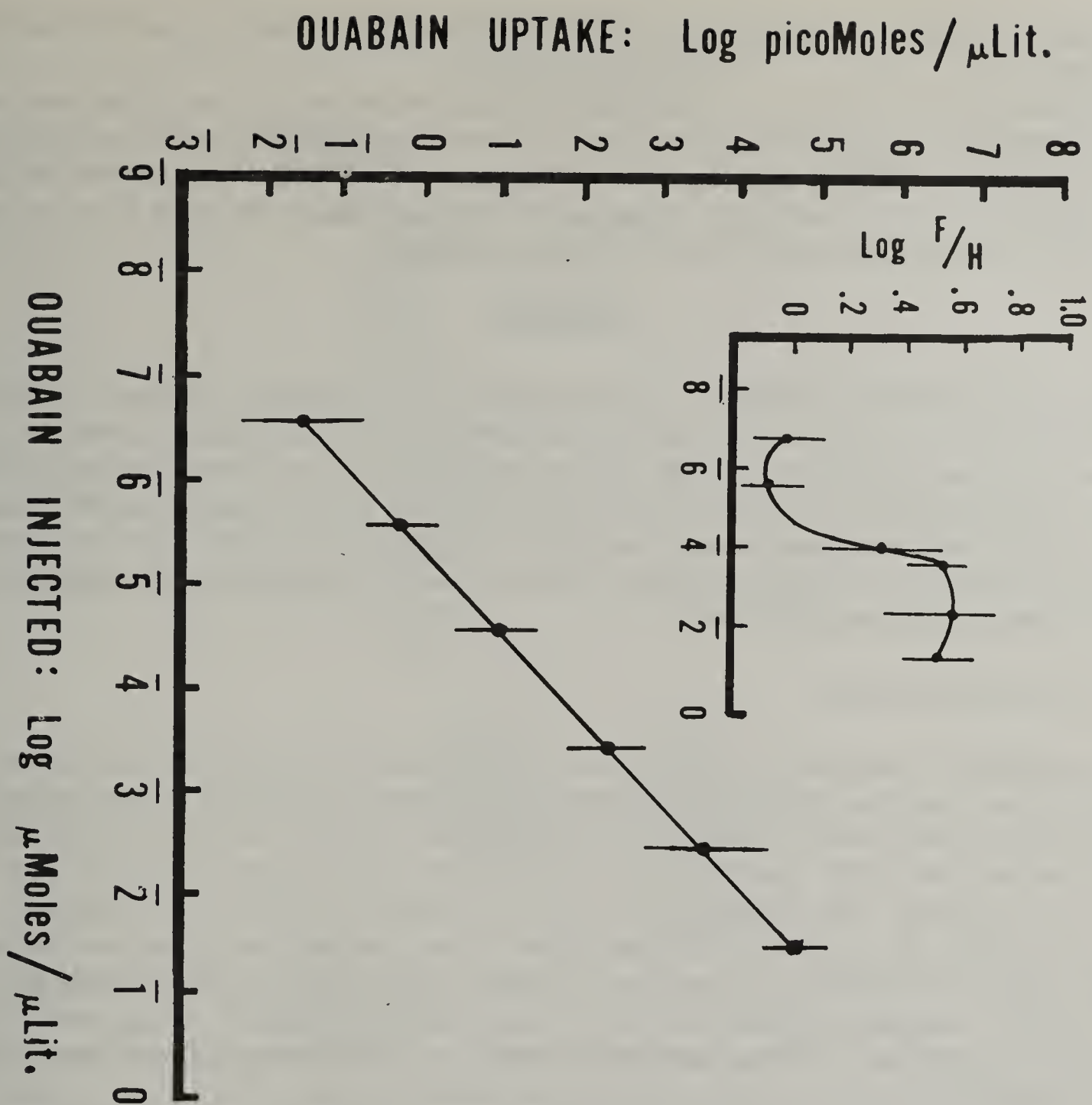


Fig. 8. – The sequestration of cardiac glycosides by the large milkweed bug *Oncopeltus fasciatus*

Ouabain uptake = uptake of ^3H -ouabain into the dorso-lateral gland fluid (see Scudder and Duffey, 1972).

Ouabain injected = amount of ^3H -ouabain injected as 1 microliter aliquots into the haemolymph.

F/H = ratio of amount of ^3H -ouabain in the dorso-lateral gland fluid compared with the amount in the haemolymph.

and density is dependent upon a feeding history with cardenolides. Interestingly, yeast cells have been shown to physically sequester ions by ion exchange principles rather than by active transport (Olsen 1969, Olsen and Tripp 1969).

The utilization of this physical process is highly advantageous for an insect feeding upon “toxic” plants like milkweed, *Asclepias* spp., for it fixes the free concentration of cardenolide in the body fluids at the critical phase forming concentration, (below toxic levels). One wonders whether other insects like the grasshopper *Poekilocerus bufonis* (vonEuw et al. 1967) and the Monarch butterfly *Danaus plexippus* (Rothschild et al. 1975) which sequester cardenolides, papilionid butterflies that sequester aristolochic acids (vonEuw et al. 1968) or even cyanogenic millipedes that store mandelonitrile, also utilize physical processes to sequester plant or their own chemicals for defense?

Considering that the sequestration of cardenolides by *Oncopeltus fasciatus* is a physical process and not dependent upon metabolic energy, aside from tissue maintenance, it is possible to question whether such adapted insects experience metabolic debt feeding upon these “toxic” plants. Brower and Glazier (1974) claim that the Monarch butterfly experiences metabolic debt while feeding on certain species of milkweeds because of the toxicity of cardenolides. The results of Erickson (1973) tend to suggest that the development of the Monarch butterfly larva is not affected by feeding upon a variety of milkweed species. This constitutes a refutation of the metabolic debt concept. The problem of metabolic debt in adapted insects feeding upon toxic plants needs more detailed analyses, especially at comparative biochemical and physiological levels. The mode of sequestration of cardenolides by

Oncopeltus fasciatus may be unique among insects, and thus a poor base to argue for the absence of metabolic debt.

Nevertheless, the evolution of a glandular structure employing the above physical process to sequester cardenolides may have been a key factor in permitting lygaeids (Scudder and Duffey 1972) to adapt to asclepiadaceous and apocynaceous as food sources. In fact, a physical process like phase formation may also be the means by which some diprionid larvae sequester plant resins in the alimentary diverticula (Eisner et al. 1975) for defensive purposes.

Conclusion

This critical review has attempted to outline some of the weaknesses, strengths, problems, and gaps of knowledge in the study of the role of allomones in arthropod biology, as well as to suggest scientific lines of attack which might in the future greatly enhance our understanding of allomones. Our present understanding of the role of arthropod allomones can be summarized by Feeny's view —" . . . a majority of land plants contain secondary chemicals which serve as defense against insect attack yet 14 years after Fraenkel (1959) gave this idea renewed prominence the available evidence for it remains meager and even ambivalent".

Language and chemical ecology

A responsibility of scientists is to communicate their findings by written language in a logical and precise manner, for their philosophy towards their science is portrayed in their experiments as well as in the terms they choose to discuss their endeavours. However, the chaotic and multifarious world is not always dissectable, and thus we are forced to attempt to describe it in the most logically uniform and convincing way possible. This is not always a problem of techniques, for our interpretative abilities can be clouded by the nature of our language or by our own subtle biases. These latter facets of scientific interpretation prompted Mason and Langenheim (1957) to write a perceptive article, "Language analyses and the concept ENVIRONMENT". I urge readers to relate the arguments presented by the above authors in relation to problem solving in the so-called area of CHEMICAL ECOLOGY.

The first concept Mason and Langenheim discuss is the *syntactic* relationship of word to word (e.g., rules of grammar). In relation to this they also stress that a word has both *intrinsic* and *extrinsic* values, the first being independent of the existence of other things, and the second being dependent upon the existence of other things and thus defining. Fortuitously, the example they chose was the word CHEMICAL. The intrinsic properties of a chemical include features such as its structure, density, physical state; however, its extrinsic properties include features such as toxicity, reactivity, nutritional value *et cetera*. These extrinsic properties actually in the contexts of ecology define the chemical; and thus, to carry the argument to the fullest extent it can be syntactically misleading to use the term CHEMICAL ECOLOGY. The adjective CHEMICAL can be interpreted intrinsically. As has been pointed out before in reference to allomones, a chemical itself has no ECOLOGY unless that ecology is defined by the physiological or behavioural responses of organisms. In essence, this means we are intrinsic rather than extrinsic thinkers. This rationale can be further demonstrated by observing the list of words in Table 6: allelochemicals, marasmins, phytotoxins, kolines (see Rice 1974), all of which describe a group of chemicals rather than a group of behaviours or physiologies. Has this terminology been a factor in producing a plethora of chemical data on allomones and a paucity of studies on how allomones work? Perhaps a nomenclature of responses would be more appropriate. However, devising behavioural response terms is no less fraught with problems as Kennedy (1972) cautions. At present most of these terms are obscurant.

Outlined in Table 6 are some of the terms used currently in CHEMICAL ECOLOGY. Some of these terms have been used for many years and other coined recently. They are employed by such putatively diverse fields as mycology, bacteriology, entomology, and botany, each with its specified or redundant usage. Many of these neologies serve only to divorce various fields of endeavour, that are striving to understand similar interactive processes. The continued encapsulation and fragmentation of the diverse responses of organisms to chemicals is intellectual frivolity. We have so many terms (Table 6; attractant, incitant, suppressant, repellent) which are used promiscuously and so poorly understood at the behavioural level. It seems futile to disguise this deficit of knowledge by a variety of circumscribing neologies which acquire an unwarranted aspect of truth and simplicity, when in fact

TABLE VI SOME VOCABULARY USED IN CHEMICAL ECOLOGY

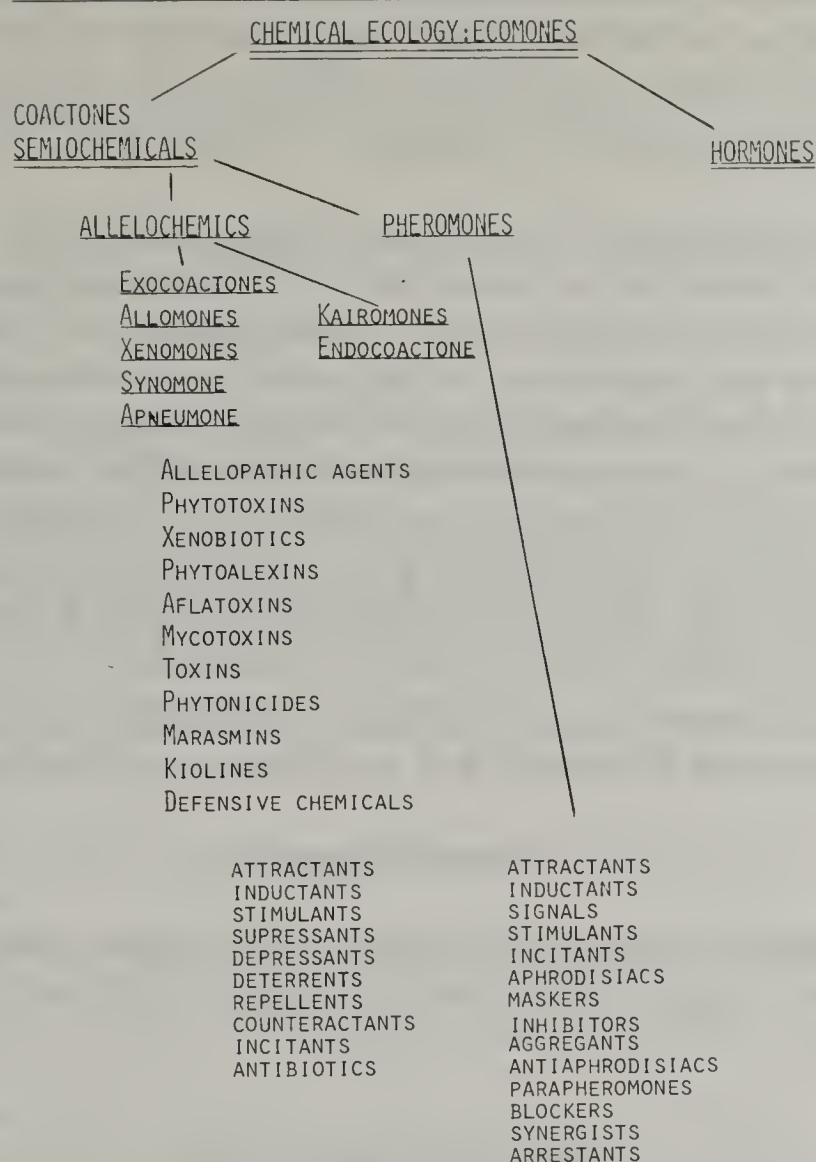


Table 6.—Continued

Terms derived from the following references: Beck, 1965; Brown, 1968; Brown et al., 1970; Chernin, 1970; Deverall, 1972a, 1972b; Florkin and Schoffeniels, 1969; Grümmer, 1955; Karlson and Butendandt, 1959; Kuc, 1975, 1972; Law and Regnier, 1971; Maxwell et al., 1972; Mitscher, 1975; Muller and Chou, 1972; Muller, 1970; Nordlund and Lewis, 1976; Raper, 1970; Regnier and Law, 1968; Rice, 1974; Schoonhoven, 1972, 1969; Went, 1970; Whittaker, 1970; Whittaker and Feeny, 1971.

they describe a vast spectrum of chemicals inducing a spectrum of changes in a spectrum of organisms in a multitude of environments. Let us first attempt to understand the words we use so casually (palatability, repellent, toxicity *et cetera*) before we burden ourselves with innumerable new terms, like synomone and apneumone (Nordlund and Lewis 1976). Do good taxonomists erect higher taxa without having an excellent comprehension of the lower taxa they are circumscribing? Such new terms can focus uncritical minds, or especially observers from other fields of science, to accept these neologies as accurate descriptions of reality. The process of naming does not render the complexity of the environment intelligible nor explainable, yet one word can disadvantageously compartmentalize our thoughts. Pretentious words are no replacement for profound thinking or experimentation.

Not all neologies are detrimental; some are of value such as the long used trichotomy of allomone, pheromone, and hormone. Even at this high nomenclatural level overlapping of function occurs. Hence, further subcategorization should be done with caution or *ad infinitum* we can describe the flea on the flea on the flea, or the *House that Jack Built*. To quote Mason and Langenheim (1957), "In semantics, as in syntactics, there has been an attempt to develop rules governing the relationship of word to the object it denotes. The first point to be clearly understood is that each of us is permitted to define his words as he chooses. Thus there is no right or wrong definition for a particular word. Through our use of them, however, words do become at least temporarily standardized in their meaning. Such usage becomes catalogued in dictionaries and then may be said to follow the rule of common usage. However, there are very important exceptions to this rule of common usage. The most important of these exceptions is where a word, standing for something in common usage, is employed so indefinitely that dissatisfaction results from perpetuation of its use. Such a word is often an inclusive term covering many confusions and hence must be clarified or avoided. It is in such cases that it becomes mandatory for the scientist to analyze the words in his

field in terms of the phenomena upon which they rest. He is then in a position to construct a precise definition. It must be emphasized at the outset that in science we are concerned with cognitive meaning, i.e., the expression of knowledge in terms of declarative sentences. Science is not involved with language expressing value judgments of feeling or emotion as in the case of meaning in the fine arts”.

“... There remains the problem of the relation of the word to the user. This is the pragmatic dimension. Because human beings design, send, and receive words, this dimension must take into account human limitations and variations thereof. Actually, therefore, it might well take into account human variations in capacity and experiences as they relate to physiological problems (limitations of perception), intellectual problems (limitations of knowledge) and psychological problems (limitations upon understanding). However, as currently developed, pragmatics tends to emphasize primarily the sources of confusion in language emanating from psychological reactions to words. The realization that most of us carry prejudices as to the extent and scope of the meaning of words can well serve as the starting point of language analysis. Once this point is recognized we then can consciously proceed to employ the syntactic and semantic rules to clarify our difficulties”. At this juncture it is important to recognize the difference between fact and hearsay, evidence and proof, and hypothesis and theory. It is to be remembered that we are all imperfect in our lessons, and therefore miscolor the world.

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Section 7: Social Insects and Apiculture

Communication and Learning in Social Insects

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Learning and Communication

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Learning and communication are among the most common and complex themes which have been developed these last years in international meetings dealing with behavior and physiology of behavior, especially at the phylogenetical levels where social life appeared with its most complicated aspects, mainly in Insects and Primates. Since we are studying in our laboratory the ontogeny of communication systems in social insects (Wasps *Paravespula*, the bee *Apis mellifera* and the ant *Formica polyctena*) and in human children (for more details, see the book "L'enfant et la communication", which will be published in 1977 by STOCK, Paris), I have thought that it could be useful to underline some convergences in approaches and aims in studies of communication systems by students of social insects and those of human behavior.

1. In man, all means of communication, even the chemical ones, are now investigated with scientific methods. Thus, A. MacFarlane (1974) found that the human neonate at 6 days of age could differentiate between a pad which had been in contact with mother's breast for 3 to 4 hours and another mother's breast pad or a clean breast pad. Our research team found that 30 to 60% of children aged from 30 months to 4 years who were given the opportunity to choose between a tee-shirt which was worn by the mother for 2 or 3 days and a tee-shirt worn by another mother, chose mother's tee-shirt in 70 to 100% of experiments, after having smelled both of the tee-shirts according to a random procedure (H. Montagner et al. 1973, 1974, 1977). Other studies are carried out on skin and sexual odours in adult man. Yet we cannot speak of pheromones, but it becomes more and more clear that specific odours can play a more important role in man's communications than it was assumed. Some workers are now trying to isolate in man's exocrine secretions chemical compounds which could act as pheromones.

2. Careful studies using naturalistic and physiological methods are now carried out on groups of children or adult human beings in free activities (for children, see N.G. Blurton Jones 1972, W.C. MacGrew 1972, H. Montagner et al. 1973, 1975, 1977). Special attention has been paid these last years to non-verbal communications inside groups. More and more students of children behavior are not just describing such and such means of communication, but rather are analysing how heterogeneous sequences of mimics, postures, gestures, touches and vocalisations can affect in different ways the behavior of the young child. In other words, more and more multi-channel communications studies inside groups of individuals are growing in this new area which is sometimes labelled as Human Ethology. INSIDE the group and MULTI-CHANNEL communication are among the most important key-words which are used in modern studies of human communication systems.

Coming to social insects, there are but a few works on multi-channel communications inside the society (among these, the well-known researches on the waggle dance of honey-bees; and Dr. A. Stuart shows an integrative approach of communication in societies of Termites). Most of studies deal with one or two means of communication and most often they are carried out in the outside world or at the edge of the society. This is necessary of course: everybody knows how much these studies have cleared up mechanisms of alarm, foraging, recruitment and mating. But we have to keep in mind that what happens in the outside world is necessarily linked to the internal life of society. Then communication studies take on truly a biological value. I am afraid that this obviousness is now too often forgotten. When considering communication inside society, and not only outside, it is clear that

each individual receives at every turn a great number of different kinds of stimuli and can himself emit different stimuli. However, according to age, time of the day, needs of the whole society, behavior of other individuals, past experiences (in T.C. Schneirla's opinion) and physiology, each individual will select only one stimulus, one kind of stimuli or a set of different stimuli. So one of the major problems of communication studies is to find how, why and when one or several stimuli become signals which orient or modify the behavior of the receiver, and sometimes his physiology, in a predictable way. Therefore it seems to me that the very sharp and careful studies which are carried out on the production of and the reactions to one kind of specific stimuli such as pheromones, sounds (Dr. J. Ishay talks about his fascinating studies on sounds which are produced in Hornets and Wasps societies), visual displays, tactile displays, must now regard, as in Primate studies, the whole bulk of stimuli and the inside life of insect societies.

The same could be said about researches on learning processes. But Dr. M. Lindauer tells us how honey-bee workers are using several physical cues together when they are training to feed outside the hive.

3. Psychological and ethological studies on Primates, including human beings, have emphasized the importance of social factors in construction of communication systems, dominance relationships and social hierarchy. But we lack of studies on the ontogeny of behavior in social insects. Yet some recent works show how it would be important to know what kind of experiences can affect the behavior of the growing organism (experiences must be taken here in T.C. Schneirla's opinion, i.e., all influences that can modify the behavior of the growing organism, whether they come from the organism himself at each stage of his development or from the outside world). Let's see one of these recent works. P. Jaisson (1975) found that when newly hatching workers of *Formica polyctena* were given cocoons of another species (*Camponotus ligniperda*, *Lasius niger*, etc.) on the first day of their imaginal life, they took care of them so that when, 16 days later, they were given the choice between cocoons of their own species and cocoons of the species they were familiarized with, they chose the last ones and destroyed the cocoons of their species. Behavior of aged imagos can therefore strongly depend on the experiences of individuals in the course of development. Now, if most of individuals undergo the same influences during development, some of them undergo different influences. That could explain why some individuals react differentially to particular specific signals, trail pheromones in ants for example, and others do not; or why individuals react in different ways to the same signal; or why most individuals are reactive to a given signal at a given time of their development and why they are not later. So it seems to me that studies on ontogeny of behavior and exocrine secretions in social insects could explain, as it is the case in Primates, differences and variations in communication of adult animals, inside and outside the society.

Differences in learning behavior could also likely be linked to social influences, or other, during the development of individuals.

4. These last years, correlations could be made between, on the one hand, behavioral profile and some situations of communication and, on the other hand, some aspects of adrenal physiology in several species of non-human Primates and in human children. For example, the child whose behavior is rich in aggression patterns and poor in motor patterns (which casually act as appeasement and solicitation behaviors) shows disturbed circadian rhythms of elimination in urines of cortisol and 17-hydroxycorticosteroids (circadian curves with 2 or 3 peaks or with a high level all along the day since the early morning (7:00 A.M.), without any significant decrease until 8:00 P.M.): see H. Montagner et al. (1974, 1975, 1977). In social insects, we know that physiology of individuals can be strongly dependent on social stimuli, for example the well-known inhibition of ovary development in honey-bee workers by queen pheromones. Conversely, some particular hormonal states (development of ovaries in honey-bee workers or in *Melipona* workers) can induce wide modifications in communication processes. Dr. H.H.W. Velthuis will speak this morning about this question. So I think that more attention should be paid to physiological correlates of communication systems.

In conclusion, modern studies on communication systems in Primates remind us that we have too often followed narrow ways in the field of communication in social insects. Conversely, studies of communication in insect societies must provide students of primate behavior and physiology of behavior with useful models: E.O. Wilson (1975) recently put us on the track.

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Some Aspects of Communication in Termites

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ABSTRACT

An account of communication in termites is given stressing the integrative approach. Particular attention is paid to recruitment behaviour and the mechanical and chemical signals involved: the results of current work on the polyethic recruitment responses of *Nasutitermes corniger* (Motschulsky) workers and soldiers to cephalic gland and trail pheromones are given. Recognition of groups and individuals and the communication involved are discussed as is the basis of attraction between groups and individuals.

A short account of current and past work on the function of head-banging behavior in *Zootermopsis nevadensis* (Hagen) is presented. It is concluded that this behaviour in *Zootermopsis* does not function in the transmission of alarm by sound or vibration. Its function remains unknown in this species, though it is possibly a mechanism that lowers the response threshold of a termite to other stimuli.

In the past decade the basis of communication in many termites has made great progress. Nonetheless, we are still far from knowing all the details of communication even in the best studied species: our knowledge is still rudimentary when compared with what is known on the honey-bee.

In this paper I shall attempt to evaluate the present state of our knowledge about how termites communicate and at the same time give some account of recent work underway. A usual way to write about communication in insects is to limit the discussion to one modality at a time and to analyse the importance of chemical, tactile, auditory and visual signals independently from each other: this is especially the normal approach of the sensory physiologist. Another way of handling the subject can be seen in the approach of Wilson (1971) who arranges the communicatory responses of social insects into nine categories such as "Alarm," "Grooming," "Recruitment" and so on. This is more preferable from the view of the study of communication (rather than physiological analysis) but the framework breaks down somewhat when the categories run into each other, as happens in the "Alarm-Recruitment-Construction" systems in termites (Stuart 1967). The same sort of difficulty arises when the physiological sensory classification when two or more different types of signals (e.g., chemical and tactile) are needed to evoke a certain behavioural response, neither signal being sufficient by itself. In termites this is seen very well in recruitment where tactile and chemical stimuli together are involved.

My approach here will be eclectic, spanning the techniques of morphology, physiology, and behavioural ecology: the subjects discussed will reflect this. The aim, in general, will be integrative in the sense of R.B. Clark (1967) where analysis by all means available is then coupled with synthesis to effect as good an explanation of behaviour as possible.

Recruitment and Its Function in Termites

That termites appear in numbers at new food sources and in response to breaks in galleries and nests has been well known for many years. A knowledge of the method of recruitment, however,

eluded investigators until comparatively recently. To obtain an aggregation at a specific location, a termite must indicate where the aggregation should occur and how to get to that place. A further refinement would be to regulate the actual numbers and types recruited. We now have a good idea how this comes about in termites, and what induces the recruitment (Stuart 1963b, 1969, 1975).

In the tropical *Nasutitermes* a colony in its carton nest may be separated from its food sources by several metres, but they are connected with them by trails, covered and uncovered. That the covered arcade is not necessary for orientation was shown as long ago as 1889 by Beaumont (1889-90) in Panama who showed that *Nasutitermes corniger* (Motschulsky) could lay open trails over pieces of paper and also that the trail was probably of chemical origin. Much later the trail in *Nasutitermes corniger* was proved to be of chemical origin and it was shown that its production occurred in the sternal gland (Stuart 1963a). At this time it was discovered that the primitive termite *Zootermopsis nevadensis* (Hagen) was also capable of laying trails and again the sternal gland was shown to be the source of production, Lüscher and Müller (1960), Stuart (1961, 1963a). In this termite, however, long trails do not occur (Stuart 1963b), as the termite lives in decaying logs and its nest is rudimentary. It was found that trail in *Zootermopsis* was principally involved in passive and active defence of the colony by causing deployment of individuals to points of excitation such as breaks in the nest, or such as happens when an intruder enters the colony. The numbers appearing at these points of excitation were shown to be nicely attuned to the initial degree of disturbance (Stuart 1963b, 1967). This happens as the excitation is transmitted by a termite which has been initially "alarmed" by its laying a trail back to the epicentre of the colony and at the same time exhibiting a characteristic zig-zag movement (Stuart 1963b) accompanied by accelerated motion. This initial excitation is transmitted to other termites encountered. Thus the trail is the directional vector in recruitment behaviour while the numbers recruited is a factor of the tactile communication of excitation. Other factors involved in determining the actual numbers recruited in any one situation will be whether one or more termites was initially disturbed, the duration of the disturbance, the intensity of the disturbance, the distance of the disturbance from the epicentre of the colony, the physiological state of the insects and the competition from other points of disturbance in the colony (Stuart 1975a). A further factor which may be involved in the numbers recruited could be the intensity of the trail itself. This could be mediated in two ways:

- (1) by the actual size of the gland and its reservoir;
- (2) by the animal having control over the amount of substance secreted. There is evidence for both these hypotheses.

Pasteels (1965) showed that in *Nasutitermes lujae* (Wasmann) the size of the gland is different in the different stages and types of workers, and that its size seemed correlated with the activity of the termites on the trail; those found more frequently on the trail having the larger glands. This is supported by the observation (Stuart, unpublished) that a trail initiated by a soldier of *Nasutitermes corniger* leaving a piece of carton on a clean glass plate is less actively followed than that of a similar trail layed down by a worker whose gland is larger.

That the animal has some control over the amount of pheromone expelled is deduced from the morphology of the gland. The cuticle overlaying the gland is studded with numerous campaniform sensillae (Stuart 1964, Stuart and Satir 1968), which must function as pressure proprioceptors which will indicate the degree of compression of the overlapping sternites forming the external reservoir. The compression of the reservoir could cause a greater or lesser amount of pheromone to be expelled (Stuart 1969), which in turn could have an effect on the intensity of trail following.

The pheromone itself has been studied in very few species. The active component in *Zootermopsis nevadensis* appears to be hexanoic acid (Karlson, Lüscher and Hummel 1968) while in *Reticulitermes virginicus* (Banks) one or more isomers of n-dodecatriene-1-ol have been shown to have strong trail following activity (Matsumura et al. 1968). Much more work should be done in this area, which is a difficult one not only from the standpoint of pure chemistry but also because it is complicated by the fact that bioassays must be meaningful and rigorous (Stuart 1970), and by the fact that the presence of trail mimics (Becker 1966, Karlson et al. 1968) means great caution must be exercised in situations where whole animals rather than extirpated glands are used as the source for extraction.

The trail coupled with mechanical communication seems sufficient to regulate numbers during recruitment. In addition, in *Zootermopsis* at least, some degree of caste selection during recruitment can occur without additional qualitative information being required. This is due to the fact that the relatively small numbers of soldiers in *Zootermopsis* are usually found near the centre of the colony.

They would, therefore, be recruited only when the initial disturbance was great enough that the excitation was passed on by the mechanical bumping to the colony centre. The fact that the reproductives are not usually recruited can be attributed to differential responses and thresholds in that caste.

In the higher termites the system of recruitment is essentially the same, with the initial excitation being often caused by the discovery of an attractive food source. In addition *Nasutitermes* is now known to have a means by which the initial excitation caused by some external factor can be amplified and reinforced by a chemical secretion from the head used in defence. Moore (1968) suggested that the cephalic gland secretion of the soldiers did cause "alarm" in addition to its well known use in defence: that of immobilising attackers due to its sticky properties. The recent work of Eisner et al. (1976) on *Nasutitermes exitiosus* (Hill) using artificial moving objects (magnetic stirring bars) to elicit discharge of the secretion by the soldiers supports that of Moore. The same phenomenon has been examined within the framework of differential recruitment by Stuart (1975a) using a different approach. The latter study using artificially presented secretions of the cephalic gland and sternal gland (trail pheromone) of *Nasutitermes corniger* to a portion of a colony confined in an inverted plastic petri dish in which a hole had been bored to permit egress, showed that the responses of individuals varied as to the context of the situation. When cephalic gland secretion was applied to the exit hole it induced a sevenfold increase in the numbers of soldiers outside the container. Without further reinforcement the numbers then fell to their original level within 20 minutes. The cephalic gland secretion, then, functions in recruiting large numbers of soldiers very quickly, but without further excitation they return to the nest relatively soon: no workers are recruited. If the trail pheromone (from a sternal gland squash or extract) is applied in a similar manner as a point source then there was again a significant outpouring of soldiers but the numbers remaining outside the nest was maintained at a much higher level and at 60 minutes after the start of the experiment approximately 50% of the maximum numbers to emerge still remained outside the nest in a tight semi-circle. Again no workers were recruited. Many more termites are drawn from the nest when the trail is drawn out from the exit but all were soldiers. Not until the trail had been drawn out (5.5 cm.) and a piece of wood placed at its distal end, were workers induced to leave the nest; at the same time the numbers of soldiers again increased. It would seem, then, that in *N. corniger* qualitative information must be communicated in certain situations to effect recruitment and that the castes respond differently to the same stimulus.

Group and Individual Recognition and Attraction

Much of the communication involved in individual and group recognition and attraction is passive in the sense that the signal is always present. This is very much the case in the phenomenon of colony odour which has been extensively studied in the Hymenoptera (see Wilson 1971). The situation in termites has been discussed by Stuart (1970), but some further remarks based on unpublished observations may be pertinent in light of Wilson's review.

Basically the test for colony odour is to put an individual from one colony in contact with an individual from a different colony of the same species and watch for signs of antagonism or other rapid change in behaviour. When this is done in *Zootermopsis nevadensis* or *Z. angusticollis* (Hagen) the initial and subsequent responses are varied according to:

1. Differences in diet;
2. Whether the test is conducted outside the colony or territory of both groups (i.e. in a neutral locale);
3. Whether one termite has been placed in the colony of another;
4. On the spatial relationships of the situation i.e., is a confrontation obligatory?

The first three situations can vary the response in degree while the forcing together of the individuals in a confined situation, or their being placed in an open situation can determine subsequent reactions. It has been hypothesised (Stuart 1970) that colony odour in termites is a medley of surface odours derived from both the environment and secretions of the termites themselves, and that an individual in a colony becomes habituated to this odour. The recognition of an alien, therefore, would actually be a "recognition" that no new odour was present. The reaction of an individual in a colony of *Zootermopsis* to any new odour, whether it be that of another colony of the same species or of an ant or of some artificial substance, is to snap, defaecate, run off laying a trail coupled with the zig-zag movement, or to investigate the source with its antennae and palps. The actual reaction of any one

termite depends on the situation (Stuart 1967). In an actual situation where two members from different colonies of *Zootermopsis* confront each other on "neutral" ground they may snap at each other or jerk, but generally the response is less spectacular than if one is actually placed in a different colony having a complement of all castes. In this case the intruder invariably excites numerous members of the invaded colony causing them to snap or jerk, and its usual fate is to be buried or consumed after being immobilised by numerous impalings on the mandibles of a soldier (Stuart, unpublished observations). Some workers investigating the same phenomena in the Hymenoptera (e.g., Butler and Free 1952) suggested that it is not the odour itself which initiates attack but rather the behavioural attitude shown by an intruder. In *Zootermopsis nevadensis* a single 12 mm. nymph from one half of a colony that had been separated for one month was placed in the other half colony. It assumed a characteristic attitude, seen many times later in similar situations, of becoming stationary, having its head stretched and at an angle of about 30° to the substrate and with its antennae outstretched laterally and beating in a somewhat horizontal plane (Stuart, unpublished observations). This attitude, however, must follow its detection by its odour and may also be a response by it to the odour of the invaded colony. It is also likely that the attitude is a response to intense grooming and investigation: a reaction less violent than might have occurred to an individual separated for a longer period.

In termites, colony odour will have the effect of partitioning the available food area without the necessity for actual attack. More usually it will cause the insects from different colonies to avoid each other and certainly in the case of *Zootermopsis* may lead to the actual construction of a barrier between two colonies. This can easily be simulated in the laboratory (Stuart, unpublished).

A situation was contrived where two groups of twenty nymphs of *Z. nevadensis* were placed in a glass covered rectangular container (6x3 inches), supplied with wood and separated from each other by wire gauze: the two groups were from different field colonies. After seven days both groups had constructed barriers of faecal material and debris sealing themselves off from contact with individuals of the opposite group. The presence of the different colonies accentuated this building. This was seen again in a situation where twenty nymphs from one colony had constructed a faecal barrier as described above. Five nymphs from another colony were then placed outside the barrier after a 1 cm. breach had been made in the wall. The five aliens were then induced to enter the breach and encounter nymphs of the main colony. Four were quickly immobilised, but the fifth exited through the breach at an accelerated pace and immediately started building behaviour (the deposition of faecal material and the positioning of debris) in a corner of the container. This continued for thirty hours during which time the animal constructed a wall approximately 15 mm long x 5 mm high effectively sealing itself off from the main colony, nymphs of which contributed to the building of the wall from the other side. There seems no doubt that the initiation of the behaviour had its origin in the communication by odour of the differences in the colonies.

Colony odour implies a general communication and recognition of all individuals as belonging to the same colony. In addition to this, however, it seems that in some colonies the presence of reproductives is recognized by the nymphs and workers or pseudergates. Lüscher (1952) showed that when conditions were altered such that replacement reproductives were formed in one half of a colony of *Kaloterme flavicollis* F. separated by wire gauze from the other half in which the original reproductives had been left, the newly formed reproductives were killed. Lüscher showed that such killing does not occur, however, if the colony is separated by double wire gauze. The inference is that tactile or surface chemical communication is taking place which advertises the presence of the original reproductives. It should be pointed out, however, that the mechanism of communication has not been determined nor has a pheromone or chemical been isolated and implicated. The situation appears somewhat different in *Zootermopsis nevadensis* where in a similar set-up the newly formed reproductives are usually tolerated (Greenberg and Stuart, unpublished).

Further instances of recognition of nestmates has been recorded in termites and Verron (1963) has implicated 3-hexen-1-ol in the cis form as causing various castes to be more or less attractive to other castes. These experiments have been discussed elsewhere (Stuart 1970, Wilson 1971), and will not be mentioned further here.

More recently attraction between the sexes of termites has had renewed attention from various investigators. In *Zootermopsis* the sternal gland has been implicated in cross attraction between males and females (Pasteels 1972, Stuart 1975b). A similar situation appears to exist in *Reticulitermes flavipes* (Kollar) where in addition unequivocal tandem behaviour occurs (Stuart 1975b), while Leuthold (1974) has shown that hypertrophied sternal glands found in *Trinervitermes bettonianus*

(Sjöstedt) imagines function in tandem behaviour in that species. Leuthold has indicated that in *Trinervitermes* the sternal gland is used in trail marking during tandem behaviour as well as (in the case of the female) a sex pheromone. This is not obviously seen in *Reticulitermes* where it has been suggested that tandem behaviour there is a response to an excitatory pheromone (Stuart 1969, 1975b).

Visual signals may be communicated in courtship behaviour of some termites such as *Odontotermes* where the female takes up a head down posture on a piece of grass and vigorously beats her wings. This appears to attract the male who takes up a position at the rear of the female, both then drop their wings and the usual tandem behaviour occurs (Fuller 1915). Again caution must be exercised, however, in assuming that the display is wholly or partly visual. It may be that the wing beating serves to disseminate a pheromone given off by the sternal or some other gland.

Other Aspects of Communication

Termites have characteristic movements that many authors believe play a role in communication. Of the three common movements known only the zig-zag accelerated movement has a known and undisputed function: that of transmitting excitation by contact (Stuart 1963b). The other two movements, "jittering" and "head-banging" as yet have no definitely known function. Howse (1964) did analyse the sound production caused by head-banging in *Zootermopsis* and on the basis of the analysis along with an investigation of the response of the subgenual organ to vibrations concluded indirectly that head-banging was a means by which "alarm" is transmitted in the colony. It has been emphasised (Stuart 1969, Wilson 1971) that the conclusions for this postulated positive feedback type of alarm of Howse are indeed based on indirect evidence. While Stuart (1963b) showed directly that a colony of *Zootermopsis* separated into two groups in a small Wilson nest by wire gauze was unable to transmit alarm from one half to the other by sound, no direct confirmation was obtained at that time that vibrations or sound were general throughout the nest. Recently this experiment has been repeated using an apparatus consisting of up to three chambers (4"x2"x3/8") with frames of "perspex" and floors variously of wood, glass, aluminum or plexiglass, stacked in a staggered fashion one on top of each other. Each chamber was sealed from the other and termites could be placed in these chambers and observed and treated separately. Vibrations present in each of the chambers can be monitored simultaneously and easily electronically. It is possible to disturb a group of termites in a lower chamber, and watch and see whether this excitation is transmitted to the groups in the upper chambers, while at the same time monitoring any transmission of sound or vibrations through the experimental substrates. When this is done it can be seen that while vibrations are transmitted to the upper chambers excitation and alarm is not (Stuart and Birch, unpublished). Other experiments where the numbers head-banging falls off rapidly after the initial response indicate that positive feed-back is not a factor in this behaviour.

While head-banging in termites other than *Zootermopsis* might prove to be important in alarm, its function in the primitive species studied is still unknown. It has been suggested (Stuart 1963b) that its purpose is to lower the threshold of the termite's response to other stimuli and so accelerate activities such as building, i.e., it modulates other signals present in the environment.

Conclusion

Much still remains to be done in the future in the investigation of termite communication. Hopefully critical analyses will be made such as von Frisch and his school have done with the honeybee (though we must remember there that a large amount of work was concentrated on a single species) in addition to the more theoretical evolutionary approach currently fashionable in the United States. Both methods are equally valid, but to be really meaningful both should be carried out in relation to each other, and each should complement each other to give us as full an understanding of the life and interactions of these insects as is possible by humans. Objectivity is paramount in our investigation of behaviour and communication in animals and the integrative approach (Clark 1967) being essentially an objective one ought to be immune from the sociological and ideological attacks that currently plague the evolutionary theorists.

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Acoustical Communication in Wasp Colonies (Vespinae)

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ABSTRACT

The rhythmic sounds detectable in the nests of Vespinae fall into two distinct categories: those produced by the hungry larvae through the scraping of their mandibles against the comb wall (the hunger signal), and those produced by the adults, mainly by the workers. Of the latter there are some which influence the activity of other colony members, i.e., the awakening taps (dance) produced very early in the morning and the taps of workers facing the queen in *Vespa orientalis*, and the ventilating noise which is a by-product of activities associated with the colony maintenance. Apart from the ventilation noise, all these sounds are produced against the comb, i.e., the various members of the wasp colony employ the comb walls as a musical instrument or a sounding board for sound production. The comb cell represents most probably a resonator, whereas the comb proper effectively distributes the sounds throughout the nest.

The sounds produced by the wasps were analyzed for their level, pattern, rhythm, frequencies and synchronization, while the combs of various wasp species were examined for their absorption coefficient values. It was found that there is a clear correlation, of a reciprocal nature, between the main frequencies of the various sounds produced in a colony, either by the larvae or by the adults, and the absorption coefficient of the comb.

The information transmitted through sounds in the nest of Vespinae is most probably pertinent to the daily problems of the various colony members.

Among social insects of the order Hymenoptera, one ordinarily distinguishes between those which construct containers for brood rearing and food storage (such as the Vespidae and Apidae) and those which do not do so (such as the Formicidae). Among the former, a distinction is generally made between social bees, which usually construct their containers out of wax mixed with various natural products, and social wasps which ordinarily construct their combs out of saliva-masticated wood products to which a certain proportion of soil is added. Although the physical and architectural characteristics of these two types of containers are different, they nevertheless have many features in common, such as the large number of hexagonal cells which make up the rigid comb, and the fact that the cells are of a relative uniform volume. From the size and the shape of a single container it frequently becomes possible to predict the caste of the brood which will develop in it. In the combs of social wasps (Vespinae) primarily two types of cells are detected (Spradbery 1973): (1) worker cells which are built in the beginning of the active season by the founding queen and later also by the emerging workers, and (2) the usually larger queen cells, which are built by the workers towards the end of the season (Blackith 1958). The third type of cells, namely those which serve specifically for the rearing of males, are not always distinguishable (Ishay 1975).

The nest of Vespinae comprises horizontal tiers of compact combs, with the cell openings directed downwards. The combs number usually between 3 and 15 and are connected to the roof of the enclosure as well as to one another by means of relatively thin columns. The shape of the nest is reminiscent of an inverted pagoda. Such nest type, with compact and relatively large combs that

allow passage of imagines only at their borders, has been designated stelocyttarous, as opposed to the phragmocytтарous nest type usually built by *Polypia* species (Polistinae) (Wilson 1971), where the combs are interconnected only at their borders and passage of the adults occurs through the center of the comb.

The nest of Vespinae exhibits both static qualities, which ensure stability, and acoustic qualities. On the one hand, the nest is insulated against noises from the outside and, on the other, it enables the creation of an informative bond between the various colony members. The interconnection of the combs by means of columns, knits the combs into one piece and thus isolates them from vibration of the ambience, which otherwise might have reduced or nullified the signals within and in so doing might have interfered with intercommunication between the members of the colony.

Most investigators have noted that the Hymenopteran insects are sensitive merely to sounds transmitted through solid media. Such sounds have been designated as solid-borne and are to be distinguished from sounds transmitted through the air, the so-called air-borne sounds. Lindauer (1961) and Wenner (1962) have noted that bees do not show a distinct response to airborne sonic stimulation but do respond well to sounds passed through the substrate, i.e., to solid-borne sounds. The same is true for ants [Adele Fielde and Parker (1964) and Haskins and Engman (1938)]. As for wasps, while it is relatively easy to pick up sounds in the nests of Vespinae, there are some difficulties in: (1) identifying the individual sounds; (2) separating them from the sounds penetrating the nest from the immediate environment, i.e., from the so-called background noise, and (3) attributing to them some communicative function.

The sounds produced in nests of Vespinae have been studied by several investigators. Janet (1895) noted that the larvae of *Vespa crabro* execute rotatory movements within their cells, while producing a distinct, clearly audible noise. Chapman (1870) deduced earlier that they were a call for food. This phenomenon was subsequently confirmed by Bishoff (1927), Duncan (1931) and Gontarski (1941) and was eventually identified by Ishay (1966) as the hunger signal of larval Vespinae. Duncan (1931) additionally mentioned the noise produced by wing-fanning wasps standing at the nest entrance. These larval and adult sounds as well as the combs of Vespinae have been analyzed for their various properties.

The aim of the present paper is to update the accumulated knowledge on acoustical communication in social wasp colonies.

Materials and Methods

Hornets and wasps: *Vespa orientalis* L., *V. crabro* L., *Paravespula germanica* F., *P. vulgaris* L., *Dolichovespula saxonica* F. and *D. media* (Retzius) (Vespinae) were all grown in special transparent artificial breeding boxes (ABB) as described by Ishay (1964). The colonies were bred under optimal conditions, and the various colony members were closely observed throughout the active hours for any sounds produced and behavior associated. Colony members were also tested for their behavioral response to the following: (1) temperatures different from the norm (Ishay and Ruttner 1971, Ishay 1972); (2) light (Ishay and Schwartz 1973); (3) sounds (Ishay et al. 1974); (4) hypergravity (Ishay and Sadeh 1975); and (5) combs whose cells differed in size from the norm (Ishay 1975); and combs which were (a) tilted by 90°, (b) tilted by 180°, (c) quartered and then glued together inside-out (i.e., with the formerly inner wall now facing out) and (d) specially fastened to prevent it from vibration (Ishay et al. 1972). All the above experiments were carried out in parallel on well-fed and starved wasps and hornets, the colonies transferred to an acoustical chamber, built particularly for the purpose of picking up their sounds. This chamber isolated external noises from the noises produced within, thus enabling the clear reception and recording of sounds (Ishay et al. 1967, Schandinischky and Ishay 1968). Solid-borne sounds and air-borne sounds were picked up by the use of highly sensitive (Bruel and Kjaer) vibration pick-up accelerometer with a linear frequency range of 5 to 25000 Hz. Recording of sounds was made either with a Revox G-36 double track tape recorder connected to the accelerometer or through a Magnetic Recording System (Hewlett Packard). Graphic representation of the various signals was either printed via polygraph (Grass) or photographed off an oscilloscope by a Polaroid camera (Ishay and Brown 1975a). The spacing of the signals was analyzed statistically (Ishay and Brown 1975b), while frequency analysis of sections of the signal was performed on a real time analyzer (B&K) (Ishay 1975b, Ishay and Nachshen 1975). The sounds were analyzed to their level, as compared to the background level, by the Impulse

Precision Sound Lever Meter, Type 1616 (B&K) Schaudinischky et al. in prep.) and to their rhythm – by either a CD C 6600 digital computer and the BMD02T program (Blackman and Tucky 1958, Ishay and Landau 1972, Ishay et al. 1974), or by an auto-correlator (Hewlett-Packard Type No 3721A Sadeh et al. in prep.). The relative sound absorption co-efficient $-a$ of the combs of various species was determined by a standing wave apparatus (B&K) (Ishay 1975a).

Results and Discussion

Except the egg and pupal stage, all the other stages of Vespinae species observed in ABBs produced sounds. For convenience, we shall categorize them as (1) sounds produced by the larvae and (2) sounds produced by the adults. Most larval and adult sounds are solid-borne and their production by one member of the colony provokes a reaction in at least another member. The ventilation noise produced by one or several adults is, however an airborne sound. A by-product of the fanning activity, it does not apparently affect the normal activity of the colony, being, apparently, of no special communicative value to any specific member of the colony.

Larval sounds have been recorded and analyzed from colonies of the following species: *V. orientalis*, *V. crabro*, *P. germanica*, *D. saxonica* and *D. sylvestris* Scopoll (courtesy of Mr. R. Edwards). Adults' tapping sounds have been recorded from colonies of *V. orientalis* and *P. germanica*. Ventilation noise has been recorded and analyzed from colonies of *V. orientalis*.

Larval Sounds

Larvae at instars 1-3 swing back and forth between the wall to which they are attached and the opposing wall. In the course of such pendular movements, they fail to touch the opposite wall because of their small size, but on the return swing their backs thump against the wall to which they are attached. Although this produces some noise, its level above the background noise was insufficiently high to record.

Larvae at instars 4 and 5 exhibit two typical movements: (a) a rotatory movement of the upper part of the body, which is usually counter-clockwise, and (b) a repetitive, frictional movement entailing extension of the upper part of the body in centripetal fashion until the mandibles touch the rim of the cell, and then contraction of the body, which causes the mandibles to rub against and along the cell wall, producing a scraping sound.

This larval scraping movement is easily seen to be invitational to feeding, inasmuch as feeding of the larvae occurs in the following sequence: the larva produces one to four scraping sounds – a worker approaches and touches the thoracic sternites of the larva with its mandibles, leaving there a droplet of masticated food or a morsel of meat – the larva immediately secretes a droplet of saliva which is picked up by the nursing worker – the larva now bends its mandibles towards its thorax, picks up the offered food and commences chewing and swallowing it.

There are periods when the scraping sounds of individual larvae are produced fairly frequently, with little interruption. Interruptions do occur once the larva is fed and the resulting pause lasts till the larva completes chewing and swallowing the food morsel. The interval between two contractions is different in worker, queen and male larvae. Worker larvae of *V. orientalis* show a tendency to contract every 3.3 seconds or multiples thereof. The increment of the larvae sound level over the background noise is unimodal in the range of 80 to 1000 Hz. The differences in levels between the maximum and the minimum amplitudes are in the range of 15 dB(lin). For *D. sylvestris* larvae, the sound level over the background noise is also unimodal in the range of 63 to 5000 Hz, but the *effective* range probably extends only between 63-1250 Hz, with the sound level over the background noise being between 7-14 dB. (Fig. 1). For *V. crabro* larvae, the sound level of the hunger signal noise is bimodal, the main peaks occurring in the range of 63-315 Hz and 800-5000 Hz. Between 315 and 800 Hz the maximal sound level over the background noise is of only 2-3 dB and is probably not efficient enough to be differentiated. In the efficient range the level difference amounts to 4-15 dB (Fig. 2). The hunger signal can also be induced by a mechanical stimulus. In such cases, the isotonic contractions of a single larva are not evenly spaced, for as the series continues, the length of time between successive contractions increases (or the rate decreases) (Fig. 3). However, the amplitude of the signal is constant for each contraction in the series. Application of repeated stimulation induces a greater response (number of contractions) to the earlier stimuli than to the latent ones (Fig. 4). This is unlike the pattern of hunger signals produced in a normal comb inhabited by many larvae. Here,

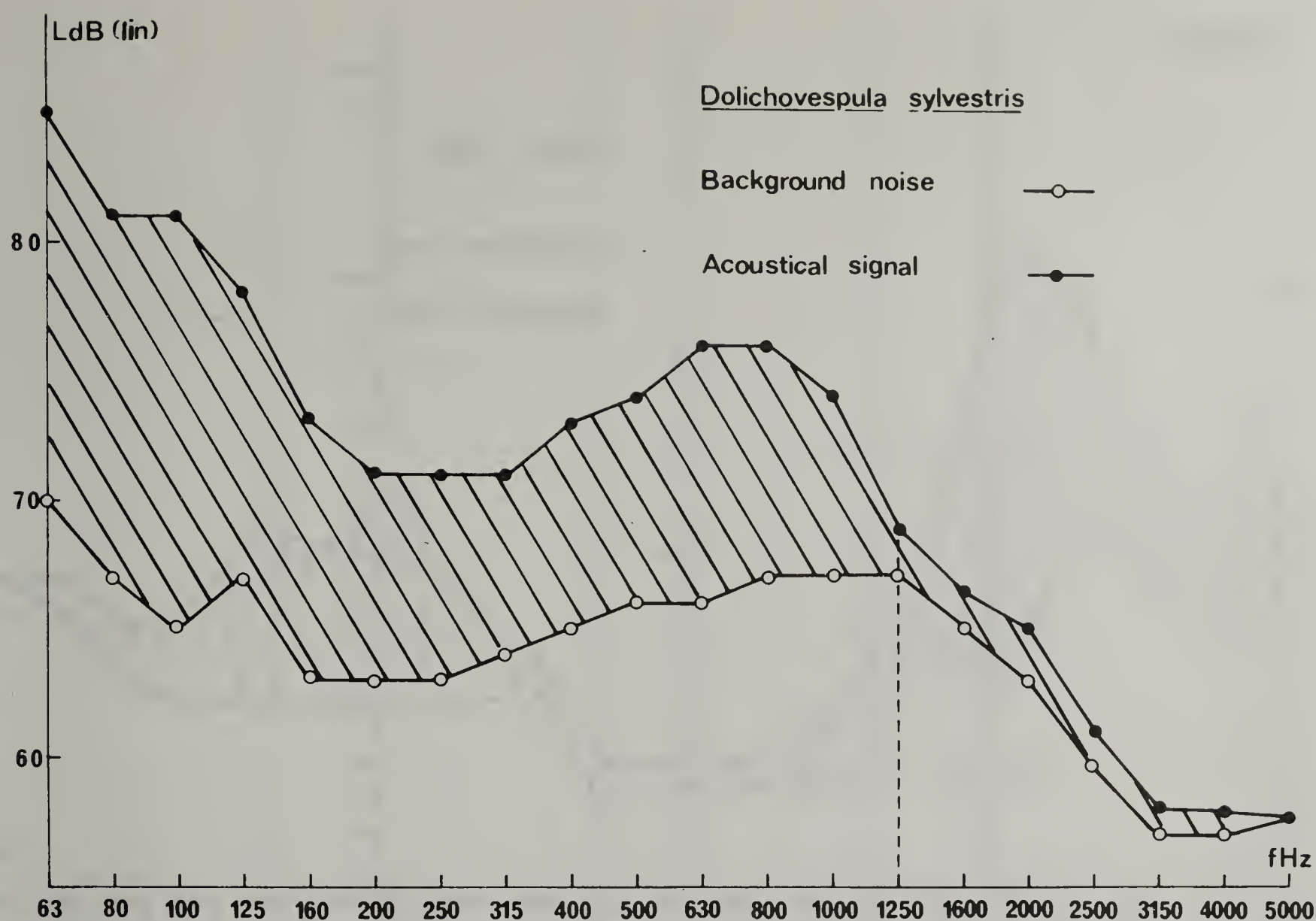


Fig. 1.— Represents the sound pressure level $L_d(\text{lin})$ of the *Dolichovespula sylvestris* queen larvae, as a function of the standard mean frequencies of 1/3 octave band. The main sound-energy is concentrated in the range of 63-1250 Hz and then decreases to very small levels. The sound absorption coefficient (α_0) is low in the above mentioned useful range.

the pattern of hunger signals is ynsynchronous for large groups of larvae, although the individual patterns may be non-synchronous. In other words, apart from the hunger signal rhythm of individual larvae, there is also a multi-group rhythm involving all the larvae in the comb, but produced by the synchronous scraping of usually non-adjacent groups of larvae. The time internal between the scraping of two separate groups of larvae is generally uniform, and ordinarily the sound rhythm of the total larval population has a frequency three times that of the individual larva. A graph of the logarithm of the power spectra estimates is shown in Fig. 5.

In Vespinae colonies, the workers usually engage in warming the pupae at temperatures below 20-22°C. In no instance were workers observed warming the larvae. Larval motor activity most probably provides sufficient heat to warm the larvae and possibly contribute even to warming of the nest. At temperatures below 20°C, however, the larvae stop producing their hunger signals and in fact they stop moving altogether. The larval hunger signals are produced most hours of the daytime but diminish during the night, suggesting a diurnal rhythm which may somehow be connected with the activity of the workers. As is known, Vespinae workers usually do not leave the nest during the night.

Larval behavior apparently remains normal under a gravitational pull higher than usual. Thus, under a resultant force of 1.5g attained by a centrifuge, the larvae continue to produce hunger signals and are consequently well nursed by the workers.

Tilting the combs at 90° or 180° to the norm does not stop the larvae from producing the hunger signals. The queen continues to oviposit in the tilted or inverted empty cells, but the workers cease nursing the larvae, descend from the comb and commence building a new normally-oriented comb underneath the tilted one (Fig. 6). If the comb is quartered and the quarters reassembled and glued inside-out, i.e., with the previously central wall now facing out, then the workers abandon three of the quarters and congregate in the remaining quarter of the comb (Fig. 7). If a normal comb is so fastened as to prevent it from vibrating, the workers cease feeding the larvae, the latter dropping out of the cells a few days later.

In another experiment, several larvae (*V. orientalis*) were starved for seven days and then offered food. The intervals between the hunger signals produced by one of these larvae are shown in

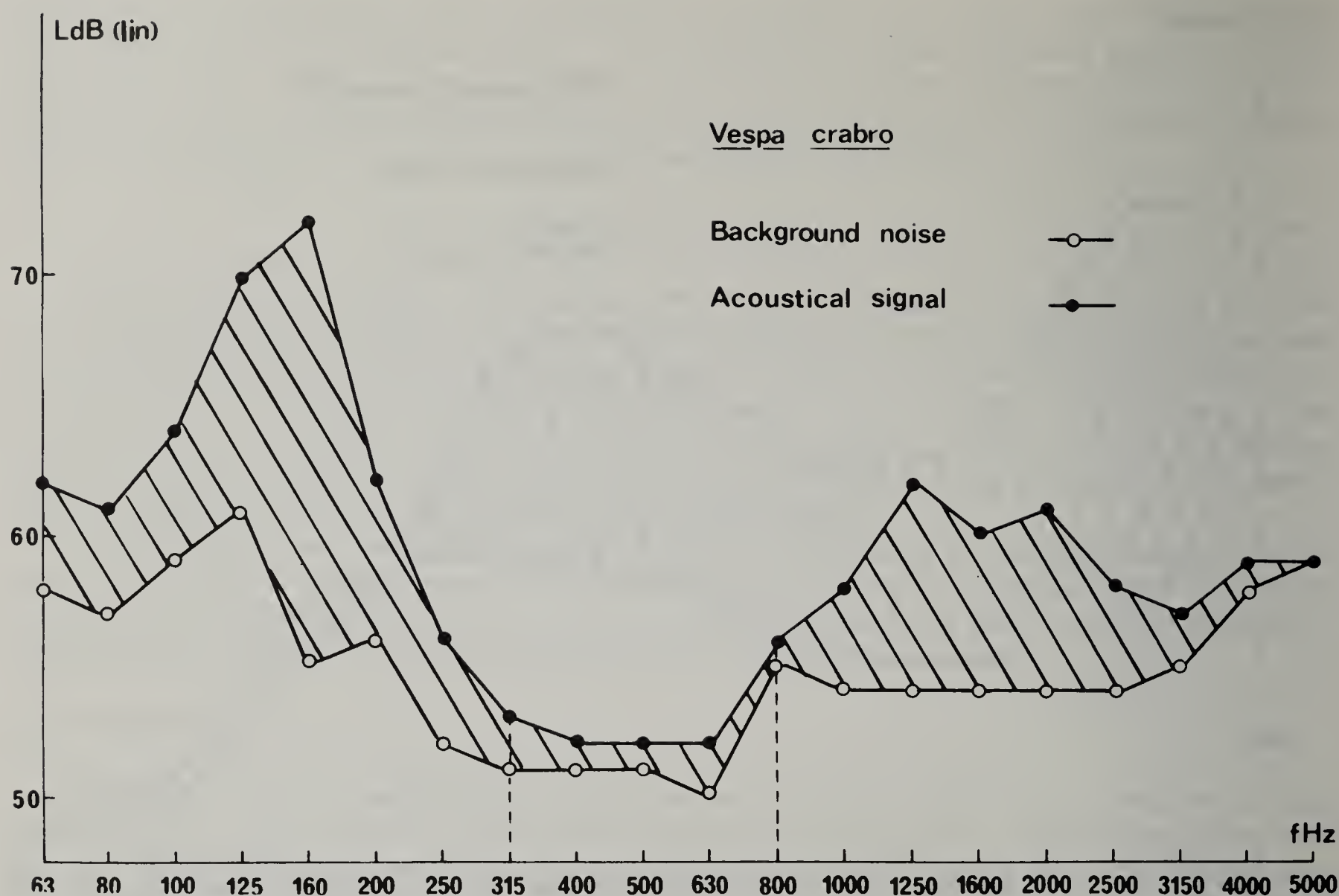


Fig. 2. — Represents the spectral analysis of the 1/3 octave bands of the sounds produced by *Vespa crabro* queen larvae. The sound energy is concentrated in two peaks: one is in the frequency range of 63-315 Hz and the other in the range of 800-3150 Hz. Sound absorption coefficient a_0 is low in the range of the first peak but the values are high in the second one; the sound absorption coefficient a_{50} has two peaks: one on $f = 800$ Hz another on $f = 4000$ Hz. The two frequency ranges of the acoustical signals occur where the values of a_0 are low. On frequencies $f = 100 - 315$ Hz, a_0 is about = 12%, and on frequencies $f = 1250 - 2000$ Hz, a_{50} is about = 40%.

histogram form in Fig. 8. The median interval between contractions was 2.60 seconds on day 5, 3.64 seconds on day 7 and 2.55 seconds on day 8 — the first day of feeding.

Do larvae produce hunger signals at a different frequency at different ages (instars)? To answer this question, I have recorded the sounds produced by three queen larvae of the 3rd, 4th and 5th instar, respectively, over a period of 3h. Each series included about 250 intervals between bodily contractions. Histograms of the frequencies of the intervals for the three queen larvae are presented in Fig. 9. As can be seen, the median intervals for the three series are 2.5, 3.5 and 2.8 seconds respectively and the distribution of the intervals also differs from larva to larva.

Daytime transmission, into a nest with a normal population, of vibrations (by means of a vibrator) at the rhythm and frequency of larval hunger signals, does not produce any detectable changes in larval activity. The workers, however, are seen to frequent the vicinity of the vibrator. When the vibrations are played into the nest during the night, the larvae “reciprocate” with their own signals, and the entire colony awakens. When the vibrator is placed and activated within one cell of a nest from which all larvae had been removed, the worker hornets pay very frequent visits to the “vibrator” cell, carrying droplets of sugar solution and/or meat morsels, which they fasten onto the vibrator rod as if it were a larva.

In another experiment, queen right colonies of *V. orientalis* and *P. germanica* were exposed to alien combs. It was found that the queen oviposits in cells that are larger than the norm but not in ones that are smaller than the norm. The workers were also sensitive to the changes in cell size and attempted to “rectify” the dimensions of those abnormal cells into which the queen had oviposited. In hornet colonies, the presence, at the start of the season, of “queen-sized” cells stimulates the workers to narrow the outlet (neck) of the cells, which results in the development of workers (Fig. 10) in the altered cells. In wasp colonies, in contrast, the workers are insensitive to cell size so long as

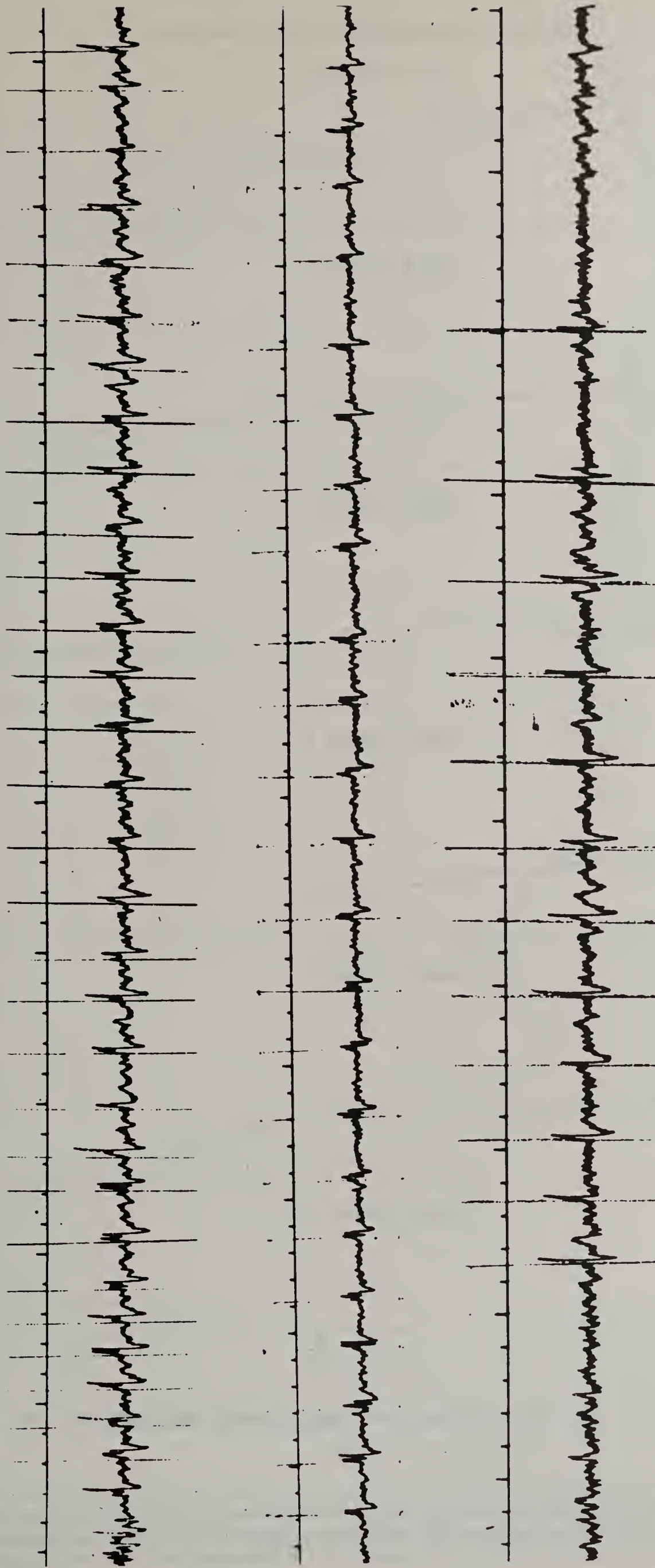


Fig. 3. — The polygraph tracing of the recordings of 3 typical series of *Vespa orientalis* larval hunger signals. The upper line in each tracing is a timer; each interval represents 1 second. The vertical lines are drawn to designate the start of the contraction. There is a lengthening of the intervals between contractions as the series continued, although the number of contractions and the absolute length of the series differ.

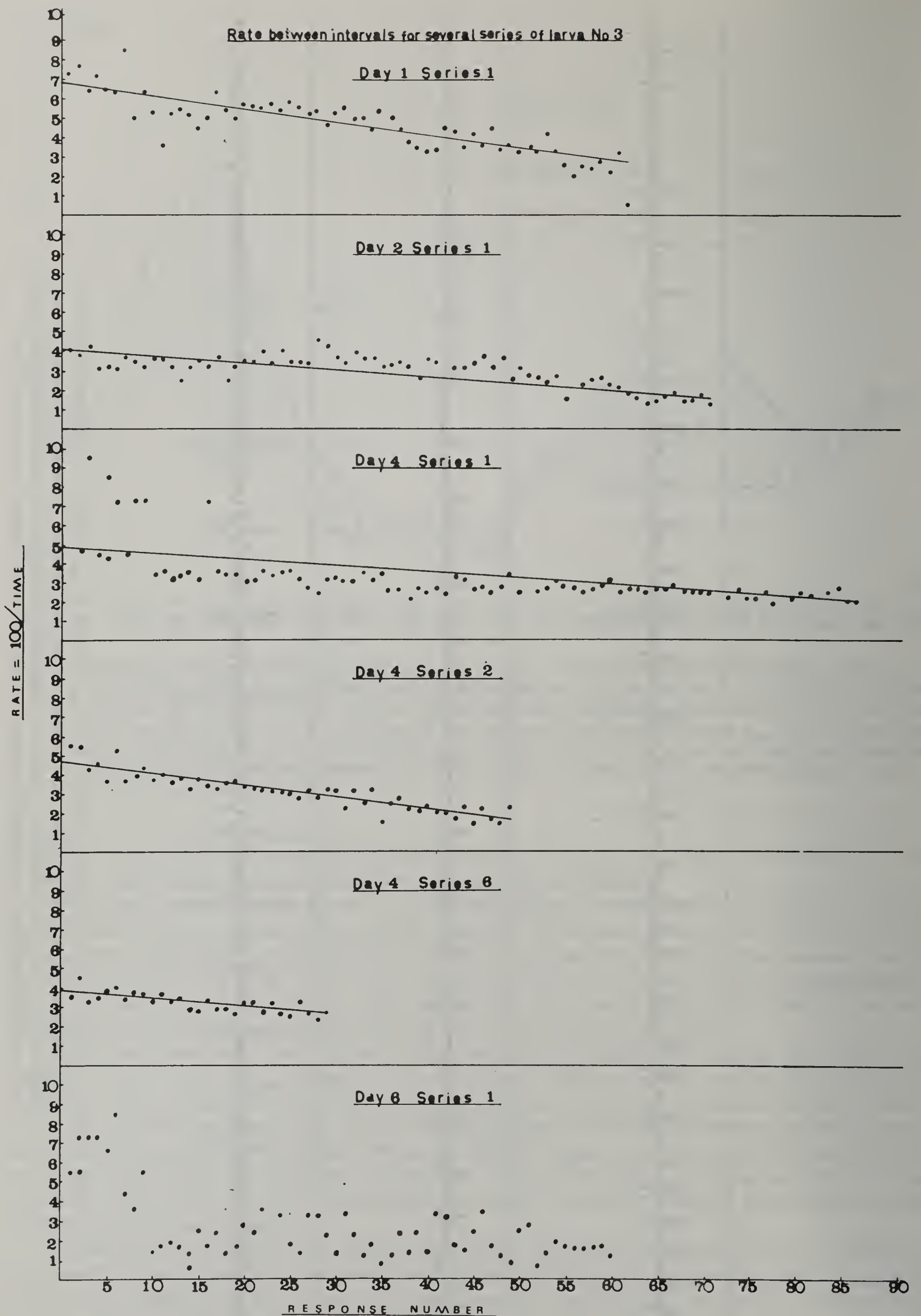


Fig. 4. — Rate of contraction (100/time, in seconds) of a larva between intervals of the hunger signal, recorded for several series on consecutive days. The straight lines represent the regression lines. The bottom trace is a sequence for which a straight line is not an adequate fit; a second order polynomial is preferable.

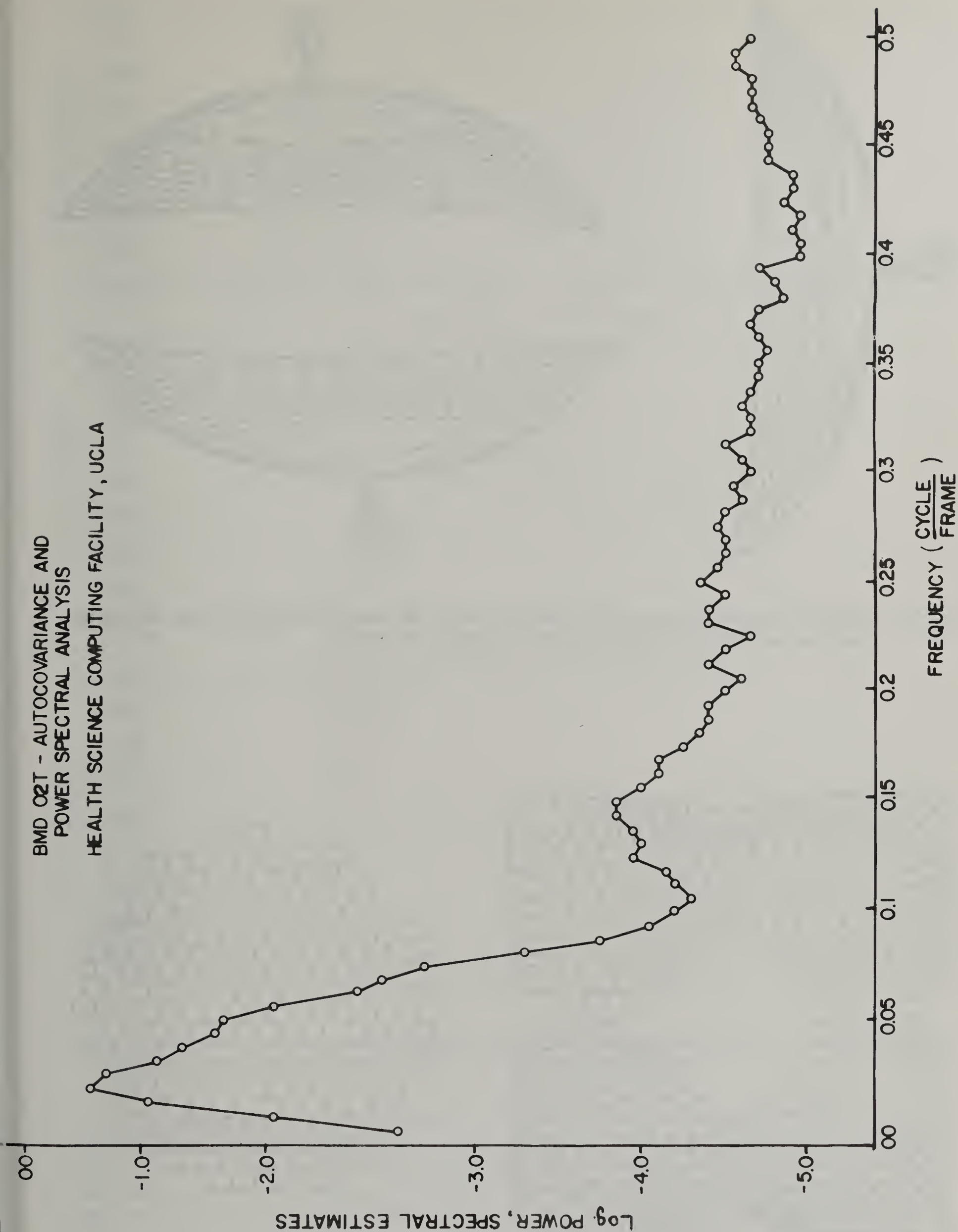


Fig. 5. — The power spectrum of *Vespa orientalis* larval contraction. The log power spectrum estimates are plotted versus the frequencies of larval contraction. The peak is significant at a 2% confidence level and indicates that this particular larva had a tendency to contract rhythmically every 53 frames (3.3 seconds) or multiples thereof.

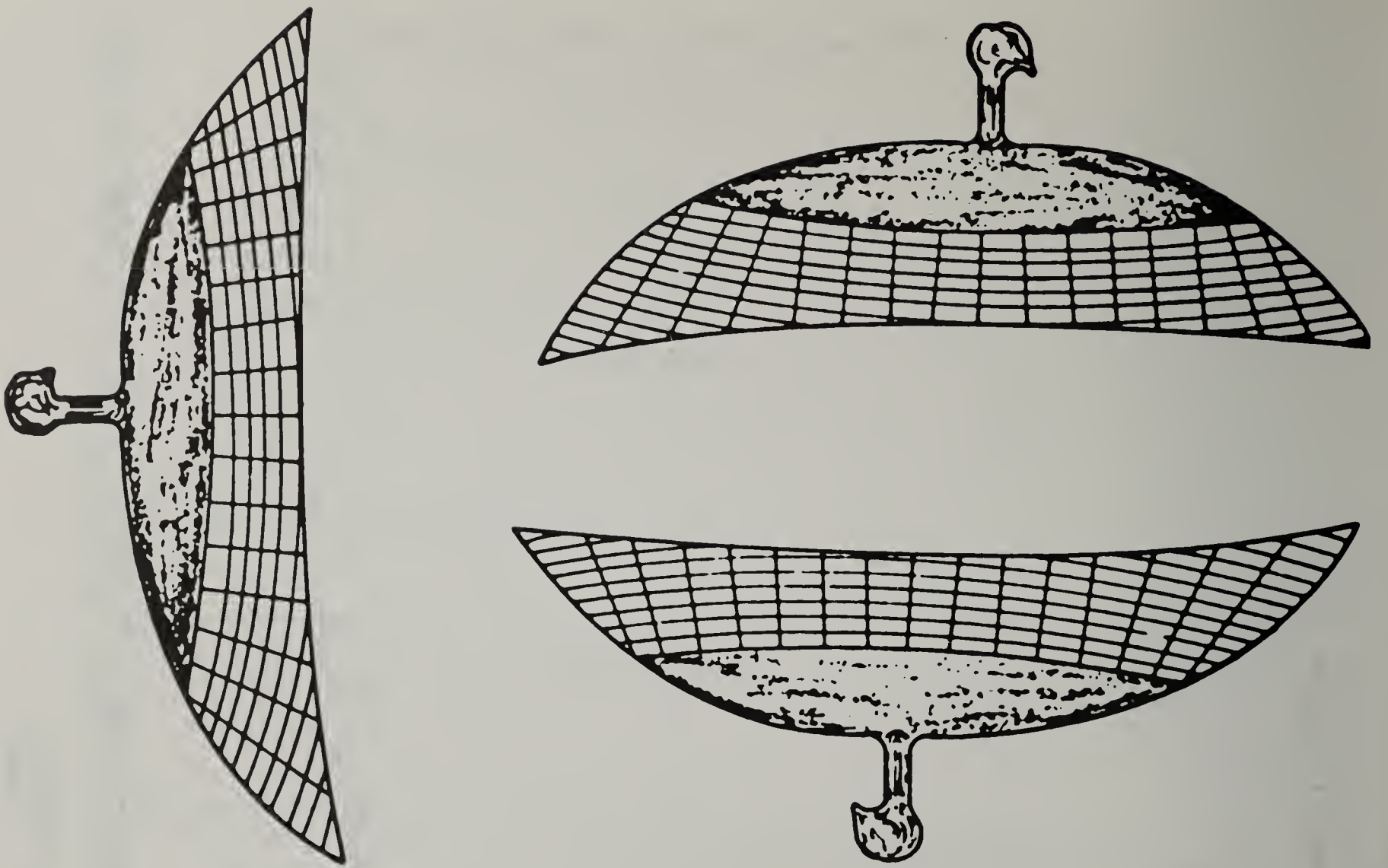


Fig. 6. – Comb in normal position (top) tilted at 90° (side) and at 180° down. This manipulation did not stop the queen from ovipositing, but the workers ceased nursing the tilted larvae.

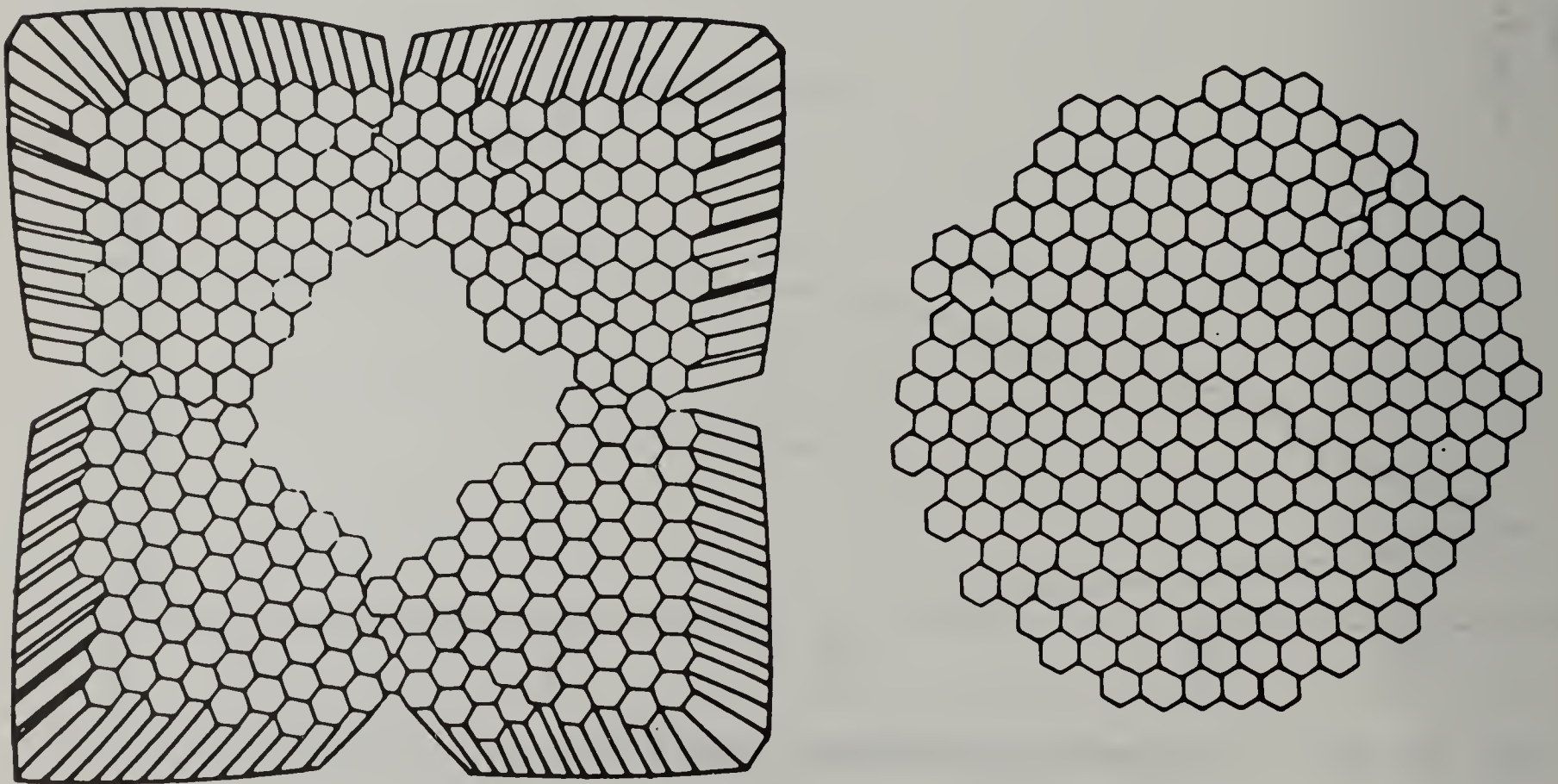


Fig. 7. – The compact built comb (left) was quartered, and the quarters were then glued together again, but inside-out, i.e., with the previously central wall now facing out. This resulted in that the workers vacated three of the quarters and congregated in a single quarter of the comb.

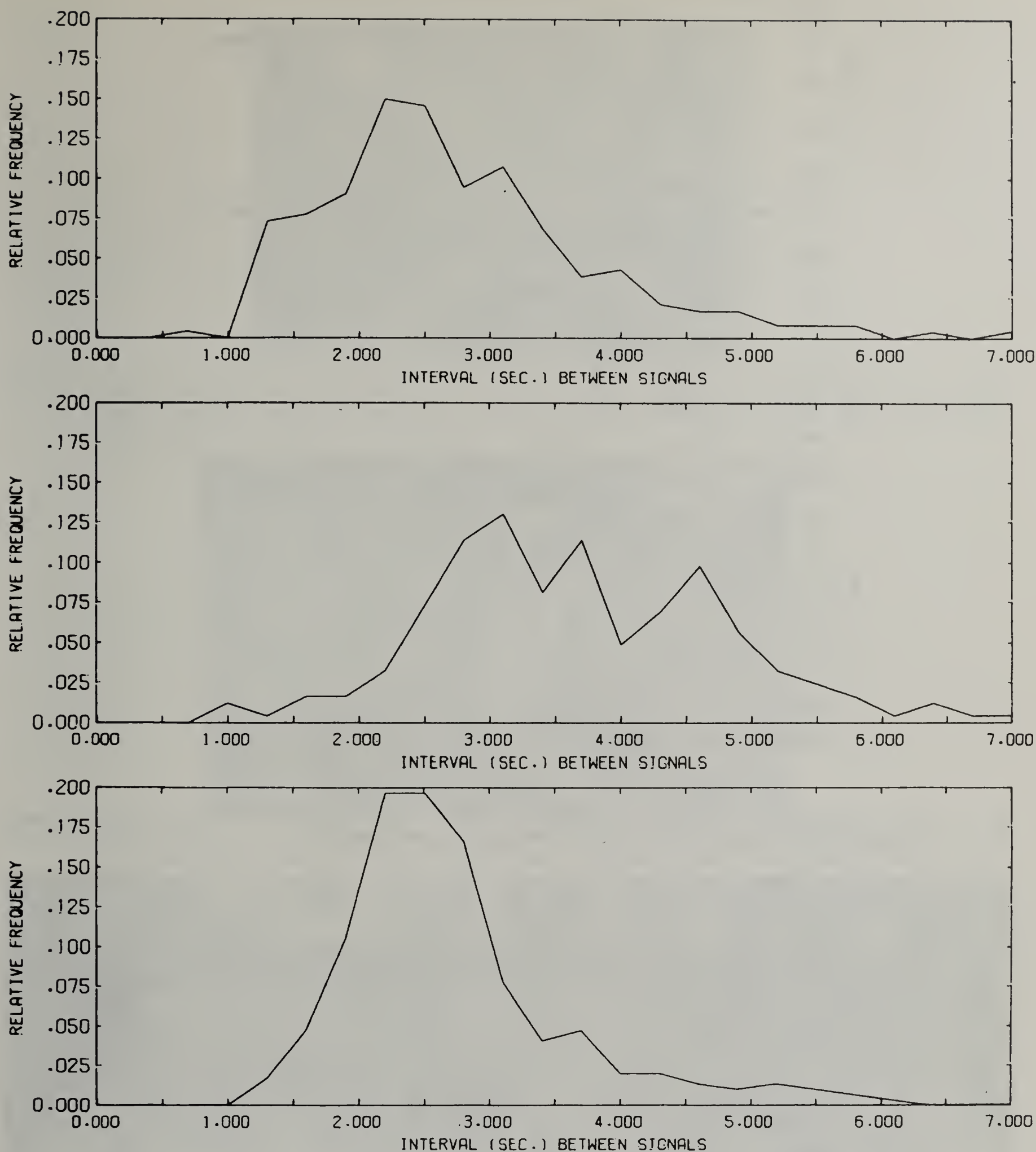


Fig. 8. —The effect of starvation on the relative frequency of larval hunger signal: top, after 5 days of starvation; center, after 7 days of starvation; bottom, after 1 day of feeding following 7 days of starvation.

the cells do not exceed twice the normal size and therefore, the introduction of a “queen-cell” comb will yield a large number of wasp queens even at the start of the season. However, if offered combs whose cells exceed twice the normal size, the worker wasps attempt to alter the cells either through a partitioning process, (i.e., reprinting) (Fig. 11), or through a cancelling process whereby the cells are plugged individually (Fig. 12) or sealed off collectively by envelope construction. The workers insulate combs with smaller-than-normal cells before they seal off the larger-than-normal cells.

Sounds Produced by Adults. — These were studied in colonies of *V. orientalis* and *P. germanica*.

The taps of workers facing the queen (in *V. orientalis*). — During pauses between ovipositions, while the queen is resting on the surface of the comb, the workers approach and arrange in a circle about her. We have called this phenomenon the resting circle. Most of the workers in the resting circle

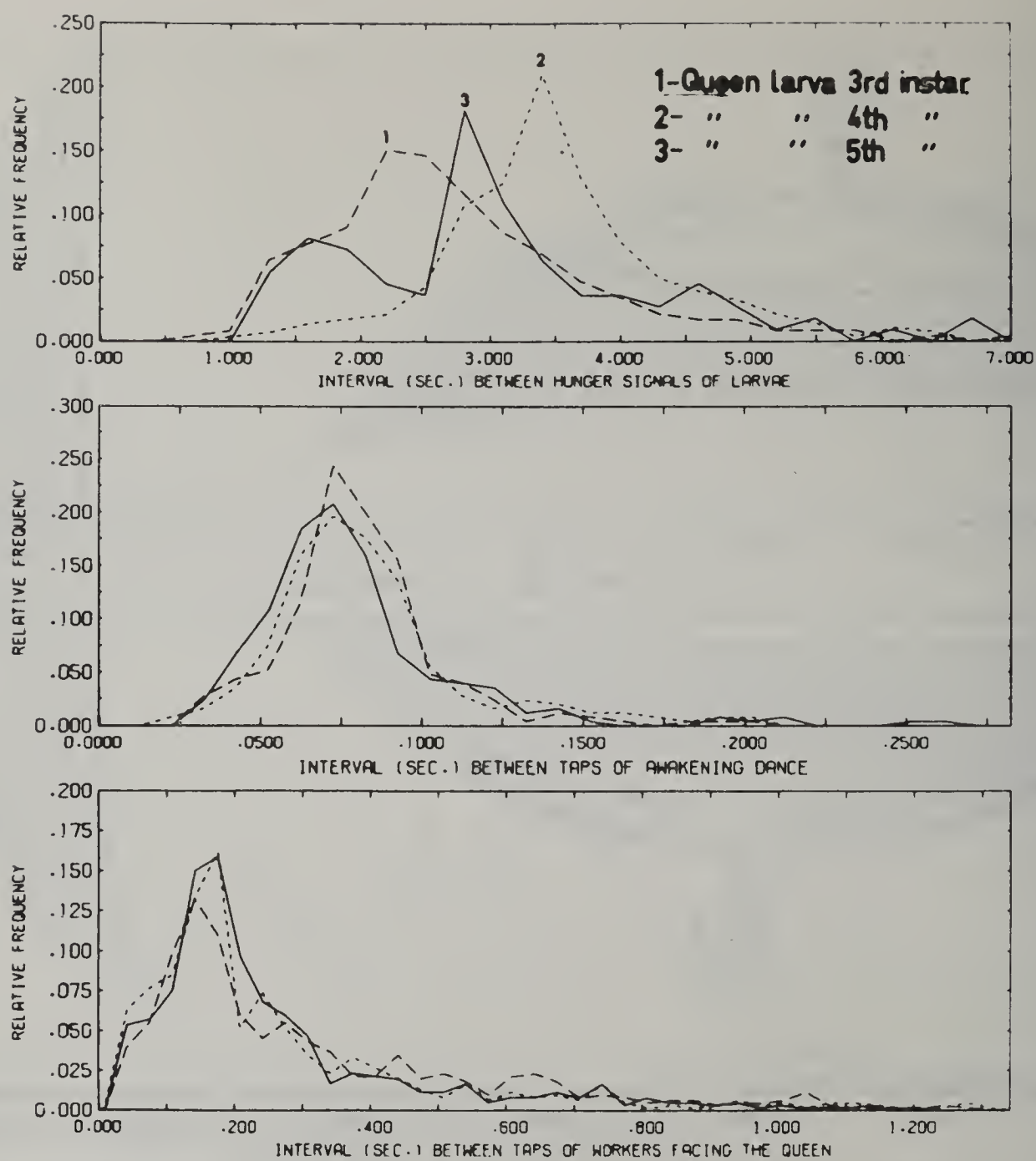


Fig. 9. — Relative frequency curves: top, hunger signals of larvae — three queen larvae of different instars; center, awakening taps of workers; bottom, taps of workers facing the queen.

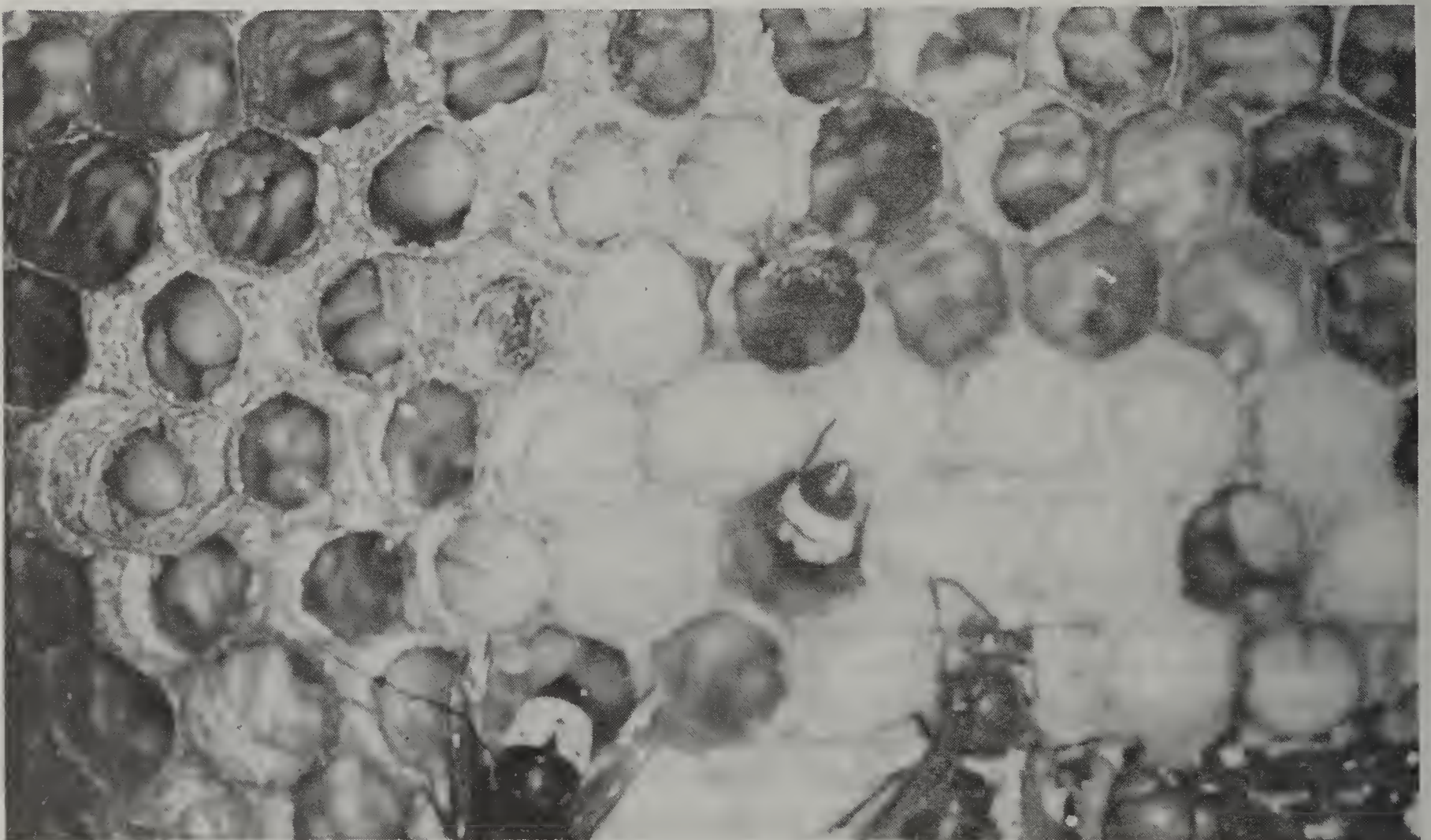


Fig. 10. — Comb with queen cells in a queen-right colony of *Vespa orientalis*. The outlets of the queen cells with large worker larvae (instars 4-5) are clearly seen to have undergone narrowing.

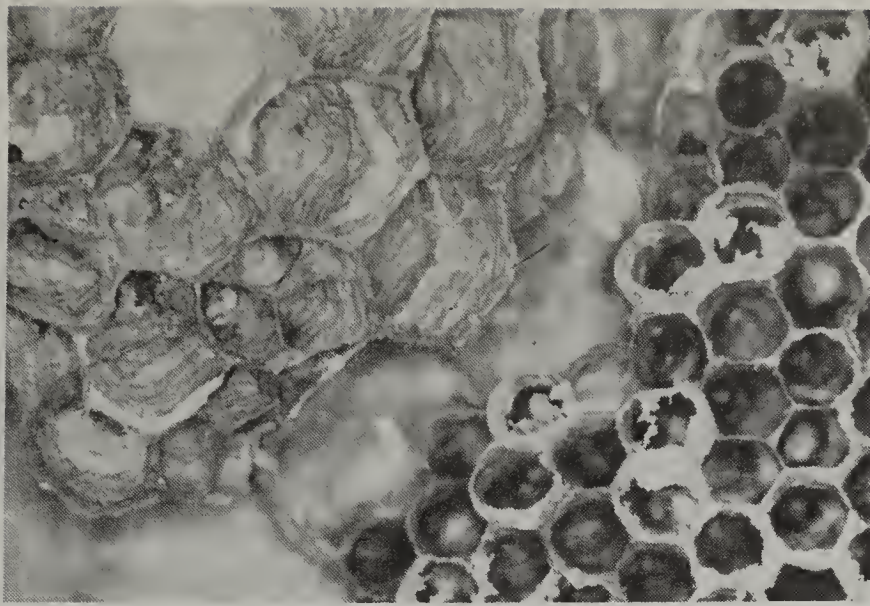


Fig. 11. — Transplanted comb of *V. orientalis* in a *P. germanica* nest. The queen has deposited several eggs within each of these cells, while the workers have subsequently partitioned these cells into two or three smaller chambers each one containing one single egg.



Fig. 12. — Queen comb of *V. orientalis* transplanted in a *P. germanica* nest. The wasp workers render such cells unfit for brood-raising by gradually constructing a plug of building material which effectively seals off their outlet.



Fig. 13. — A queen in a *V. orientalis* colony surrounded by workers in a typical resting circle. The workers standing against the queen proceed to lick the head of the queen and to tap with the abdomen against the surface of the comb.

proceed to lick the body and particularly the head of the queen, but one or two commence tapping their abdomen against the surface of the comb (Fig. 13). These tapping sounds, although produced within the nest, are clearly audible outside it, even at a distance of 1-1.5 meters. Frequency analysis of the sounds reveals that they are rhythmic, unimodal, peak in the region of 80 to 500 Hz, decrease rapidly until 1250Hz, differ from the background noise by a maximum 12 dB and from the background noise by 1 to 10 standard errors. Two series of taps were clearly recognizable from the various recordings. In the first series there were several 'hard' taps which were followed by a number of alternatively 'hard' or 'soft' taps. The time interval between two consecutive taps was 0.3 seconds during the first and about 0.15 seconds during the second series. The intervals, however, were not absolutely fixed, varying within a range of $\pm 30\%$. The mean time intervals are given in Figs. 14 and 15. The sounds are usually produced in the morning hours, in well populated colonies, starting from the month of July. As mentioned earlier, the tapping workers are few, usually only one and very rarely more than two. They are at least 5 days old, have apparently smaller-than-average body measurements and for several successive days they do not leave the nest. The tapping lasts for at least as long as the queen rests and often continues after she has started to move. When artificial vibrations of a similar rhythm and frequency are sounded in a colony, they produce several effects: (a) The queen starts moving over the surfaces of the combs or between the combs, apparently in search of vacant cells for oviposition; (b) The workers which had been arranged in a 'resting circle' around the queen resume their usual nursing or other duties; (c) Hunger signals of the larvae cease immediately after the first few vibrations and are not resumed even if the artificial vibrations are continued without interruption for as long as 30 min. To emphasize the significance of this latter finding, we point out that towards the end of the summer, the norset nest contains combs with approximately 2000 to 2500 brood-filled cells. The majority of cells are 'occupied' by larvae of the 4th-5th instar, which ordinarily produce hunger signals during the most hours of the day. Nonetheless, the moment the artificial vibrations are 'played' at the appropriate rhythm, all larval movement and hunger signalling ceases. The tapping sounds may be brought to a stop by the introduction into the nest of volatile alarm substances, but in no instance are the tappings to be regarded as alarm sounds or as providing information pick-up *outside* the nest because the tapping workers do not leave the nest for days.

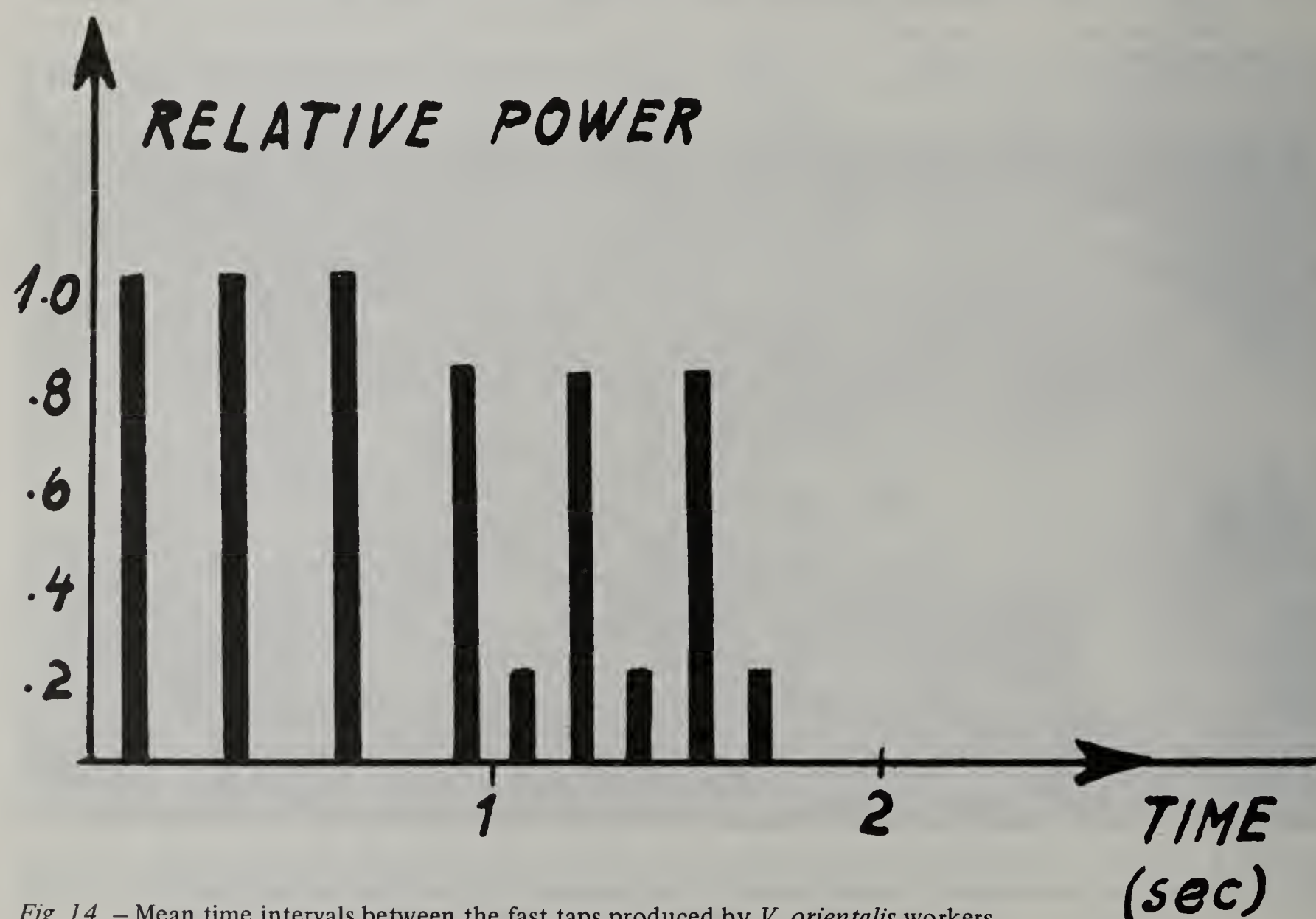


Fig. 14. — Mean time intervals between the fast taps produced by *V. orientalis* workers.

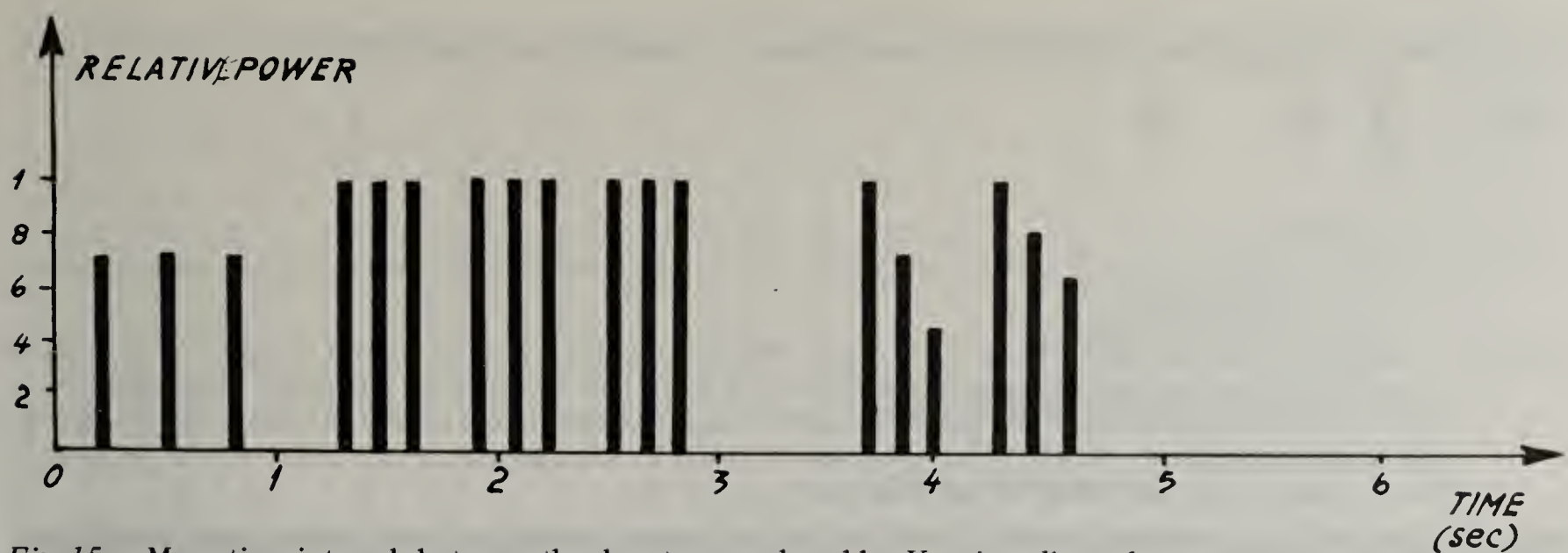


Fig. 15. — Mean time intervals between the slow taps produced by *V. orientalis* workers.

Dance of awakening (in *V. orientalis* colonies). — When at night a shaft of bright light is directed into a hornets' nest grown inside the vesparium and in which movement has almost completely ceased on account of the darkness, a few workers that in daytime serve as 'nurses' to the larvae begin to beat their belly upon the walls of the cells. After executing a number of quivering abdominal movements — what we have called the 'dance of awakening' — they insert their heads into cells housing larvae and proceed to "milk" them for saliva. Doing this repeatedly they soon awaken the entire colony with their activity. Other, apparently foraging, workers now proceed to the nest entrance to all intents set upon going out into the field. The larvae, in turn, start emitting hunger signals and the whole colony commences behaving as if in daytime. The awakening dance noise has a unimodal peak in the region of 80 to 500 Hz and decreases rapidly until 1250 Hz, so it does not differ in this respect from the tapping of workers facing the queen. The awakening dance, however, shows a different pattern: it occurs in bursts separated by intervals of rest. These bursts were measured and found to last 1.25 to 2.50 seconds, with a mean of 1.81 seconds (Fig. 9 middle). The peak of the spectrum appears at 0.012 cycles per ms, that is, at a frequency of twelve taps per second. The peaks are highly significant ($p < 0.005$). It should be emphasized that: (1) the awakening dance is a natural, daily phenomenon in every colony, being performed spontaneously by a few workers in the early morning hours; (2) the dance is in no way related to any kind of alarming insofar as (a) it cannot be induced during the daytime, i.e., directing a shaft of light during the day into the nest, does not alter the colony's normal activity, (b) following it most of the workers engage in nursing the larvae rather than in a search for intruders as is customary during alarming situations.

Sounds produced by Adult *P. germanica*. — During most hours of the day, but particularly in the late morning hours, noises are frequently heard from colonies in the vesparium. The noises comprise tapping sounds produced in series of 20-60 beats, each beat consisting of 15-30 sub-beats (Fig. 16). By carefully removing the wrapping of the nest, it becomes evident that the noise is produced by workers who tap their abdomen against the cell wall or against the comb pedicle. Usually, after a worker starts its tapping, a second worker and, at times, a third, soon joins in a short distance (2-10 cm) away from the first. At the beginning the sounds produced by each worker are easily distinguishable, but after several beats they tend to merge and are recorded almost as one prolonged beat (Fig. 17). This appears to be the result of synchronization of the beats (taps) of the two wasps, every double beat protracted and containing twice as many sub-beats as the single beat. As for the beats in each series, we were able to determine the time interval between two successive beats, the period of quiet between two beats and also the complement time, i.e., the duration of substrate vibration as a result of the sub-beats. In the longer series of beats, the serial correlation with the substrate vibration time was high. For the interval between primary beats, the coefficient of variation was high but the serial correlation was low. This suggests that the substrate vibration may occur in a definite pattern which could therefore have communicative value in itself. There is a high correlation between the number of sub-beats and the substrate vibratory interval (which, of course, is to be expected) and this lends support to our conclusion that the substrate vibratory interval is the most important of the three time variables: (1) time interval between beats, (2) quiet time between beats, and (3) time of substrate vibration.

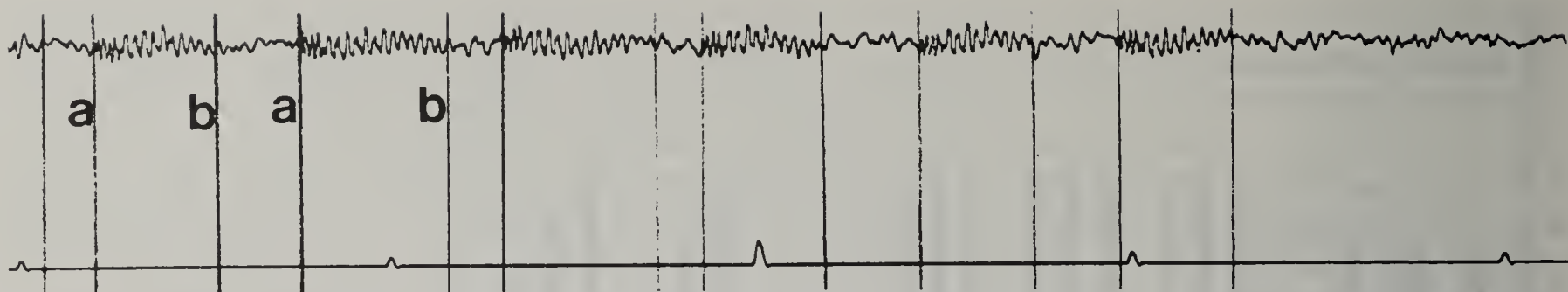


Fig. 16. — A segment of the end part of one beat of a *P. germanica* worker speeded up by a factor of 16 (top plot) vis-a-vis time in seconds (bottom plot) as picked up from tape recorder on polygraph. Proceeding from left to right, one can discern the onset of a subbeat (a). The substrate is caused to vibrate by rapid waves which gradually decay, enabling the substrate to revert to baseline quietus (b). After a brief interval, a second sub-beat sets the substrate vibrating anew, and so on.



Fig. 17. — Oscilloscopic tracing of beats produced by two workers simultaneously. Every double beat is prolonged in time. Each square represents 2 seconds.

The frequency analysis of the wasp comb and of the sounds produced by the wasps is shown in Fig. 18. As can be seen from the figure, in the range of frequencies above 80 Hz, the relative sound level of the noise of two wasps tapping simultaneously is higher than that generated by one wasp alone. The relative increase over the background of the sound level produced by two wasps tapping simultaneously is double that of a single wasp. For purposes of comparison, the maximum of the relative sound level attained by one wasp, in 1 min is also shown. We believe that the doubled beat may be tantamount to emphasis or intonation and represents a phenomenon of temporal summation.

The differences between the relative sound level and the background noise increase from 50 to 1000 Hz for two of the cases: one wasp alone and two wasps simultaneously (Spearman rank correlation $r_s = 0.82, 0.65$; $p < 0.01, p < 0.05$, respectively). After 1000 Hz the differences decrease and disappear altogether above 2500 Hz. The pattern of the sounds produced by *P. germanica* generally resembles, but is more rapid than, the sound pattern of the awakening dance of *V. orientalis*. It remains to be seen whether the beats produced by the wasp workers in their nest serve a similar function.

The Ventilation Noise. — It is a common tendency of different species of social wasps to maintain a fixed temperature in their nest. When the ambient temperature differs markedly from the optimum, the wasps try to correct the situation by various 'passive' or 'active' methods (Ishay 1973). The wasps actively warm the pupae even outside the nest, at temperatures between 18°C and 27°C. We found that pupae that matured at temperatures of 20°C or lower, eclosed with malformations and were of low viability. During normal development the pupae lose weight as shown in Fig. 19. We recognize here a kind of 'drying out' process, which is of decisive importance to the pupae maturations. This drying out process is essentially accomplished by a continuous and intensive evaporation of the body fluids of the pupae, comparable to the intense perspiration of human beings and other mammals. The evaporations from the pupae diffuse into the nest ambience rendering it

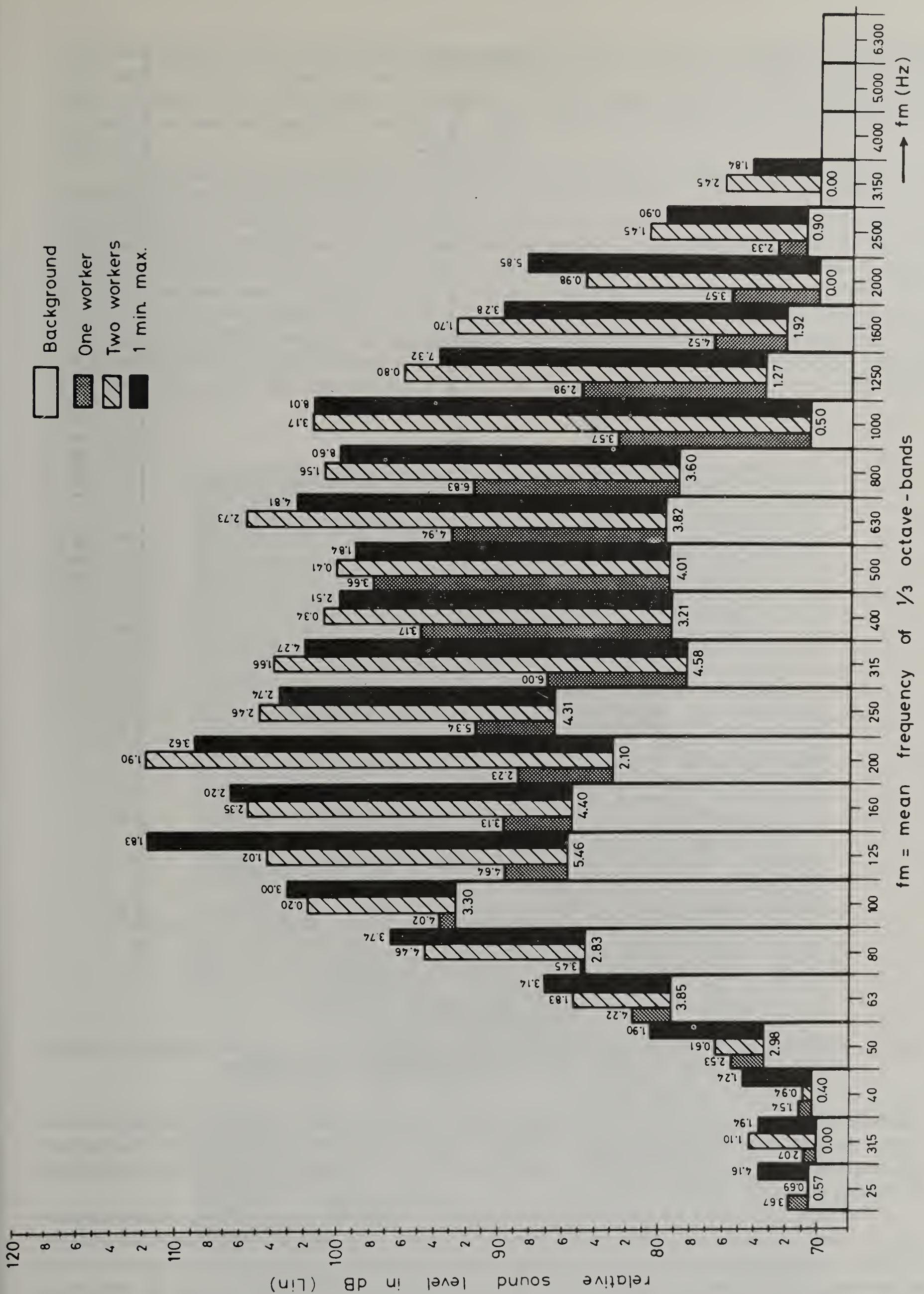


Fig. 18. - Spectral analysis of the sound frequencies via real time analyzer. Top bars represent the noise produced (1) by one single wasp (*P. germanica*), (2) by two wasps simultaneously; and (3) maximum noise produced by one single wasp in 1 minute. Background noise is given underneath. The numbers above represent the standard deviation values of the wasp noise, while those below are the standard deviation of the background noise. Results are mean values of three separate recordings of single wasps and background and of ten recordings of two wasps simultaneously.

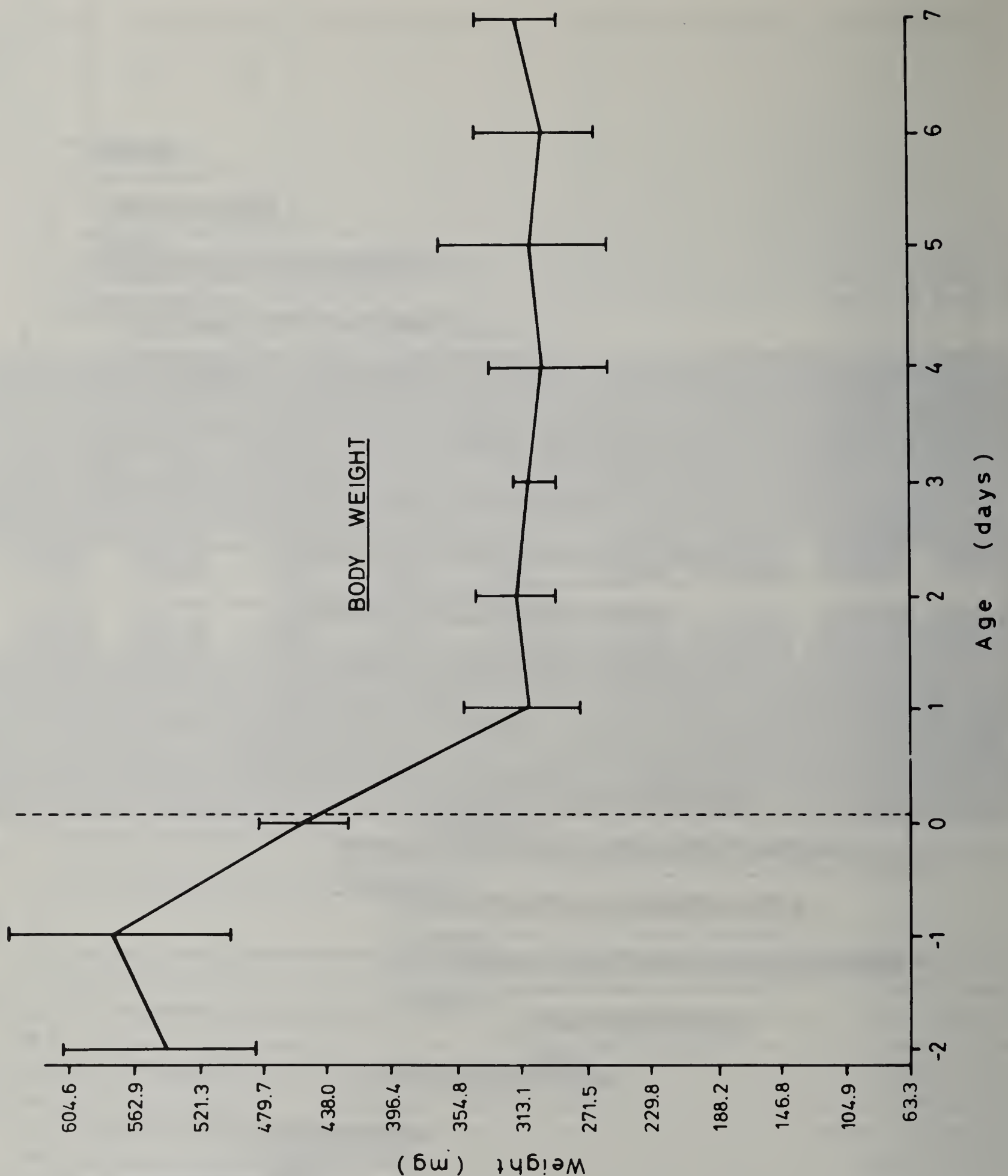


Fig. 19. – The reduction of body-weight of pupae (age -2, -1=days before hatching) and young imagines as a function of the age in days (day 0 is the day of hatching). Limits indicate standard deviation.

relatively more saturated than usual and after a while, with additional evaporation of liquid from the pupae, the ambience becomes harmful to wasps. The so-called ventilation activity of the workers prevents this from occurring by creating a continuous flow of air in and out of the nest, ensuring also the 'drying out' of the pupae.

The fanning workers are most frequently dispersed on the outside of the nest, at some distance from the entrance, but may also arrange behind and around it, in the galleries between the entrance and the combs, and on the combs proper. The ventilating workers are spaced 2-3 cm apart so as not to obstruct traffic of hornets in and out of the nest. During the ventilation activity the workers all orient themselves in the same direction, with the head facing out (Fig. 20). Ordinarily the topmost ventilating workers do not extend beyond the nest entrance, but in very populated colonies or at the end of the season, when the soil around the nest has become moistened by rainfall, some ventilating workers may situate themselves 20-30 cm outside the nest entrance. In ABBs it was found that some

of the ventilating workers concern themselves exclusively with ventilation, carrying out this activity over a period of up to 7 minutes, after which most of them leave their fixed position and retire to rest inside the nest. Most of them return to ventilation activity several times during the same day. Some workers were observed engaged in ventilation activity 17-30 times a day, and for at least 4 days in a row.

The ventilation noise produced by the workers during the day or night has been analyzed, using a Frequency-Spectrometer, at the 1/3 octave band level in dB(lin) as a function of standard mean frequencies (fm) in the range of 63 to 6300 Hz. In parallel the appropriate background noise was also analyzed (Fig. 21). At daytime we have found (in *V. orientalis*) two pronounced peaks: the one at 80 Hz (fundamental), the other at 160 Hz. Both peaks surpass the background level by about 10 dB(lin) having an absolute value of approximately 60 dB(lin). At night the corresponding peaks 'shift' down by about 1/3 octave, reading 63 Hz and 125 Hz respectively. The peaks of nocturnal sound levels are also lower by 5 dB(lin), being about 55 dB(lin). In a previous paper (Schaudinischky and Ishay 1968) we noted that the two pairs of wings of *V. orientalis* do not beat synchronously, but rather each wing pair beats with a short time-delay after the other. The fundamental wing frequency must therefore be

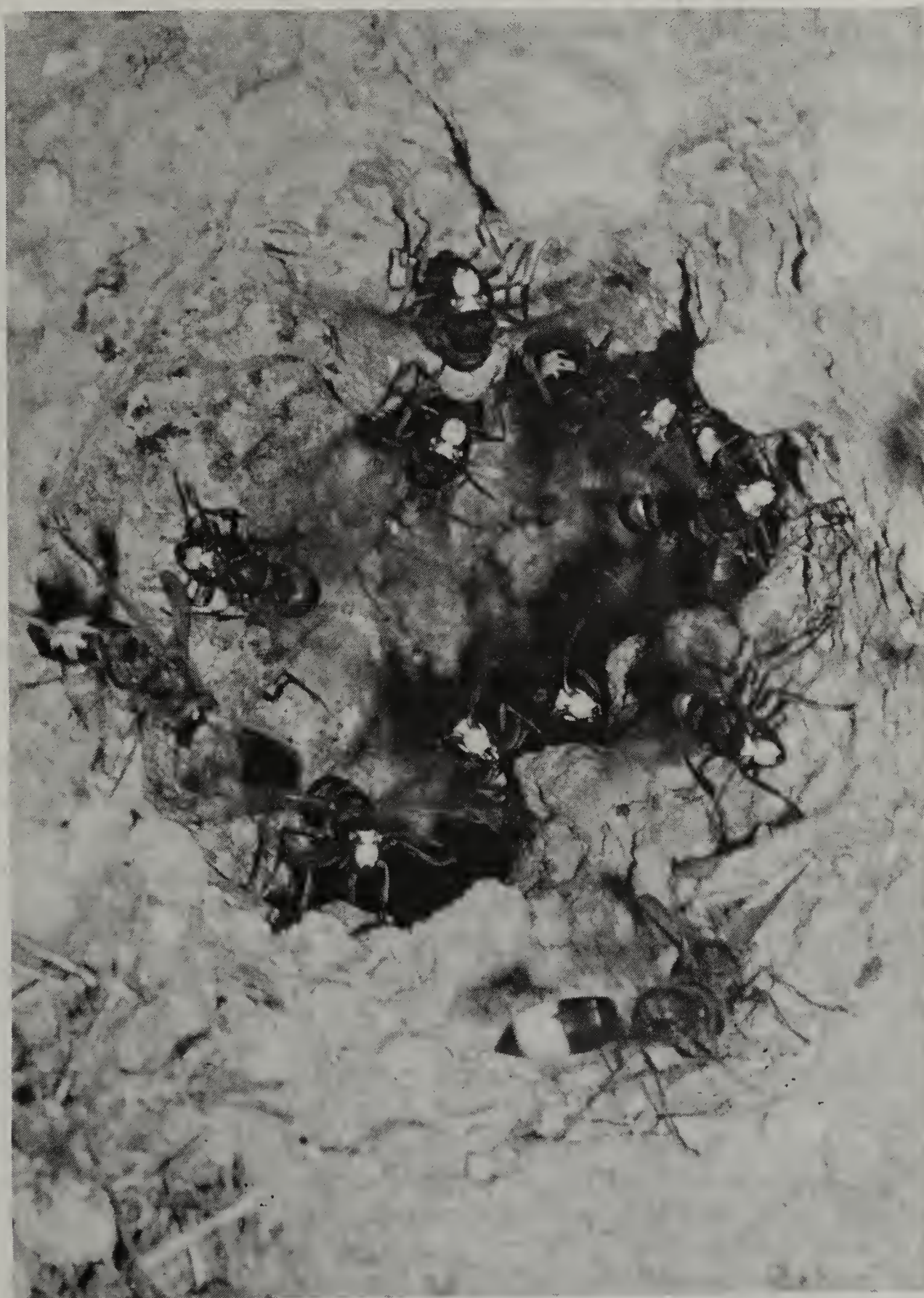


Fig. 20. — Ventilation work. Workers (*Vespa orientalis*) sitting in an approximate circle around the entrance of their nest, steadily fanning their wings.

divided by two and, hence, the real “day” frequency is about 40 Hz and the “night” frequency is about 31.5 Hz. The ventilating workers arranged in rings around the nest entrance and are thus comparable to the preparation of small-point sound sources around a circle. This in turn leads to the possibility that at very high frequencies ($f > 10,000$ Hz) another array might perhaps be produced, which serves foraging workers on their flight back to the nest as a kind of “guide beam” (Fig. 22).

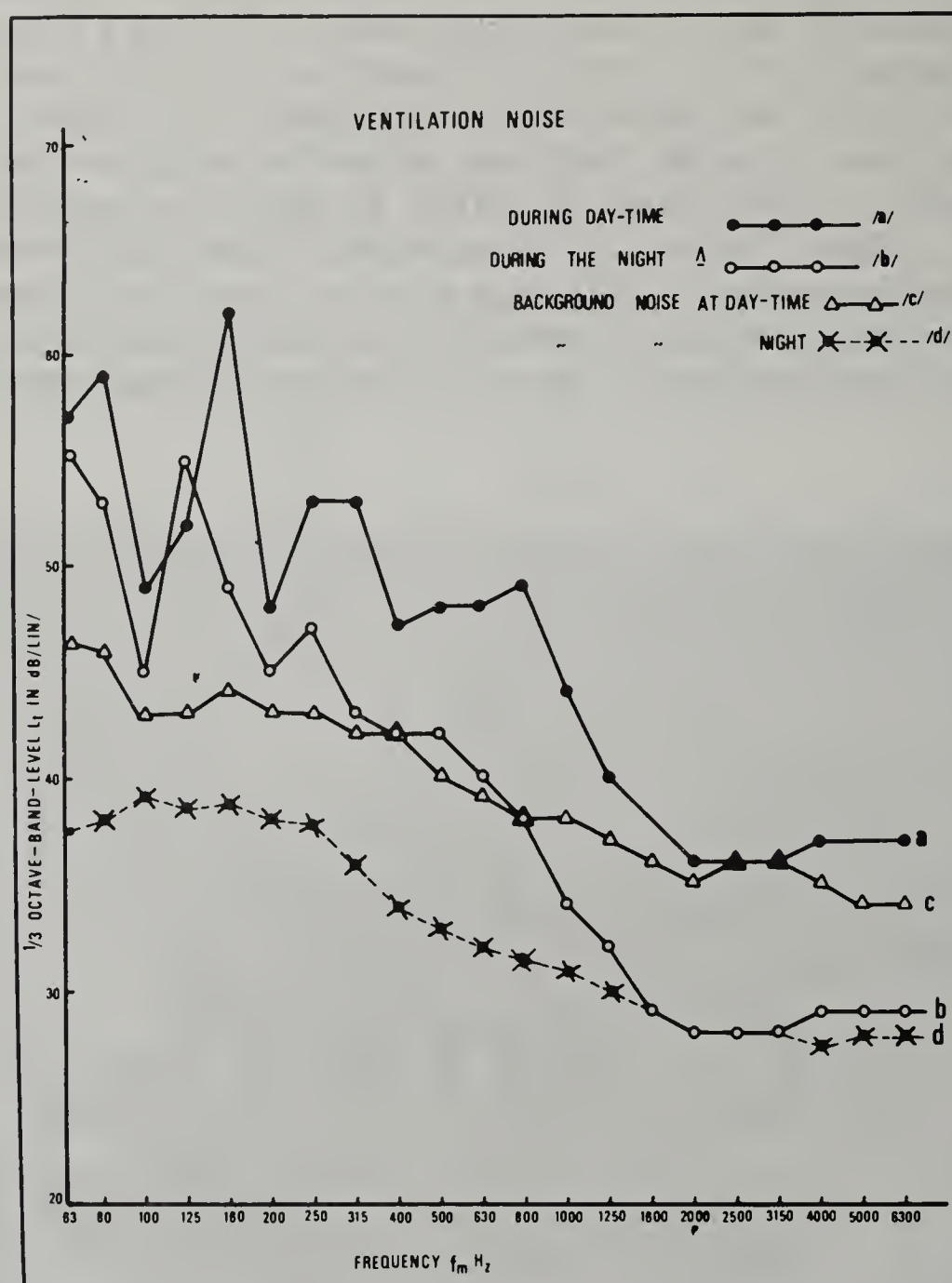


Fig. 21. – The third octave band level L_t in dB(lin) on the noise, caused by the ventilation activity as a function of standard mean frequencies of 1/3 octave band. $L_t = f(f_{mx})$ dB(lin).

In order to obtain accurate data on the fanning activity and the noise produced by it, we fed the recordings of individual hornets, from start to finish of the fanning activity into an auto-correlator (Hewlett-Packard Type No. 3721A). The main advantage of the auto-correlator is that it can extract a repetitious signal out of a random noise which may be much larger than the signal itself. A second advantage is that the time-measuring capabilities of the instrument are very precise, enabling to determine the rate of repetition with maximum accuracy.

The top curve in Fig. 23 illustrates the result of such an analysis (at 28°C and 90% relative humidity). A representation of 33 1/3 ms of real time is displayed. It shows a clear repetitious signal occurring every 6 2/3 ms, or 150 times per second. In terms of wing movement this implies that downstroke-upstroke beat of equal intensity occurs every 13 1/3 ms, or 75 times per second.

An interesting change is noted about 6 minutes after the workers start ventilating. The change is evident from the middle curve of Fig. 23, which is different from the upper curve in two respects: the strokes occur at a somewhat faster rate (153.8 times per second or every 6.5 ms) and every second stroke (probably the down-stroke) is lower in amplitude (by 32%) than the first. Five minutes later, the pattern is altogether different (Fig. 23, bottom curve): the down-stroke is still there, but is split into three peaks, and the upstroke is also split into three. The time between two upward strokes is now shorter (12 ms, or 83 1/3 times per second). This new pattern is interesting and is probably detectable only with a correlator. It shows that at a certain moment, probably when the hornet is

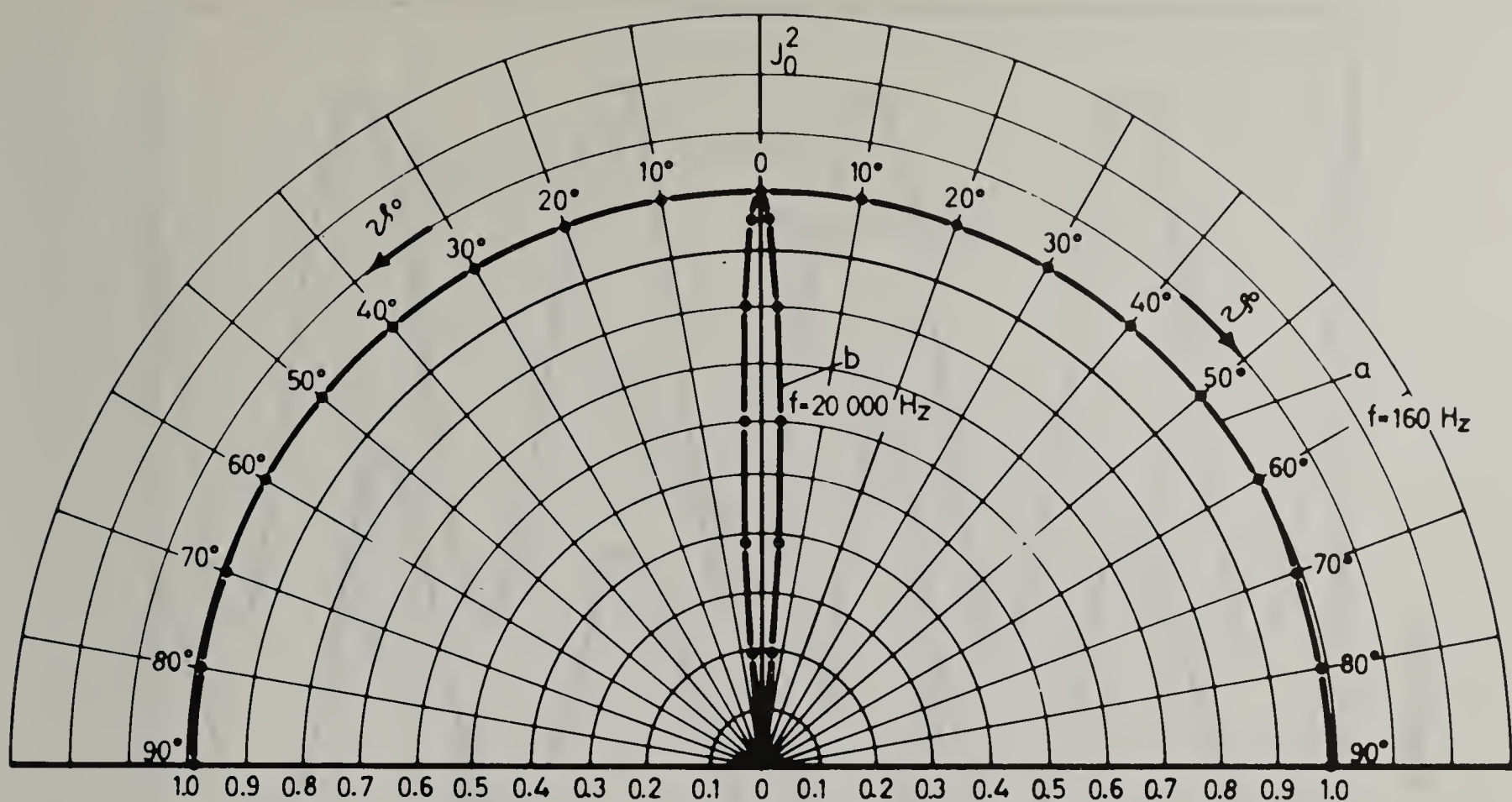


Fig. 22. – Polar characteristic of the sound emitted by a “sounding circle”. Curve “a” shows the sound energy as a function of the angle in degrees as received by a hearing mechanism. We recognize that for a low frequency ($f=160$ Hz) there is practically no difference in sound-energy, if the perception occurs under any angle ϑ from zero to 90° ; curve “b” is drawn for high frequency sound ($f=20,000$ Hz). Here, the directivity of the emitted sound is of a beam-like sharpness. A minor derivative of the frontal perception of the sound. Waves, already causes an extremely high drop in sound energy. At the angle $\vartheta = 7^\circ 29'$, τ_0^2 becoming zero.

tired, the down-strokes are not made in one continuous swing, but are rather divided into three shorter swings before the upward stroke commences. The reason we suspect hornet fatigue to be responsible is that the total energy expenditure in the bottom curve is smaller than in the middle or top curve. The energy content values of the peaks in Fig. 23 are presented in Table 1:

Table 1

	Top curve	middle curve	bottom curve
Down-stroke	100%	79%	21%
Up-stroke	100%	55%	12.5%

It should be noted that in the natural, well populated nest, a considerable number of workers (up to 30-50 on every warm day or following rainfall) may be engaged in ventilation activity. This poses the question (now under investigation), as to how the ventilating workers synchronize their wing movements to avoid a phase difference which would interfere with coordinated ventilation.

As is to be expected, the dynamic flight noise frequency of the workers is 1.25-fold higher than the static ventilation noise frequency. Furthermore, it is quite clear that the muscular effort necessary for flight is essentially greater than that for ventilation activity. Our results show that the flight-energy is 10 times as great as the energy needed for ventilation (Fig. 24).

In order to find out if there is any correlation between the acoustical properties of wasp and hornet combs and the sounds propagated in the nest, we have measured the absorption coefficients of the combs and compared them to the frequencies of the sounds produced in the nest.

Figure 25 shows the sound-absorption-coefficient α_0 as a function of 1/3 octave band mean frequencies, of a comb with worker brood. The air distance was chosen as $d_A = 0$ cm, i.e., the sample examined (piece of comb) was placed close to the end of the standing-wave tube. As the curve demonstrates, α_0 is nearly constant in the frequency range of 100 to 1600 Hz and the average value

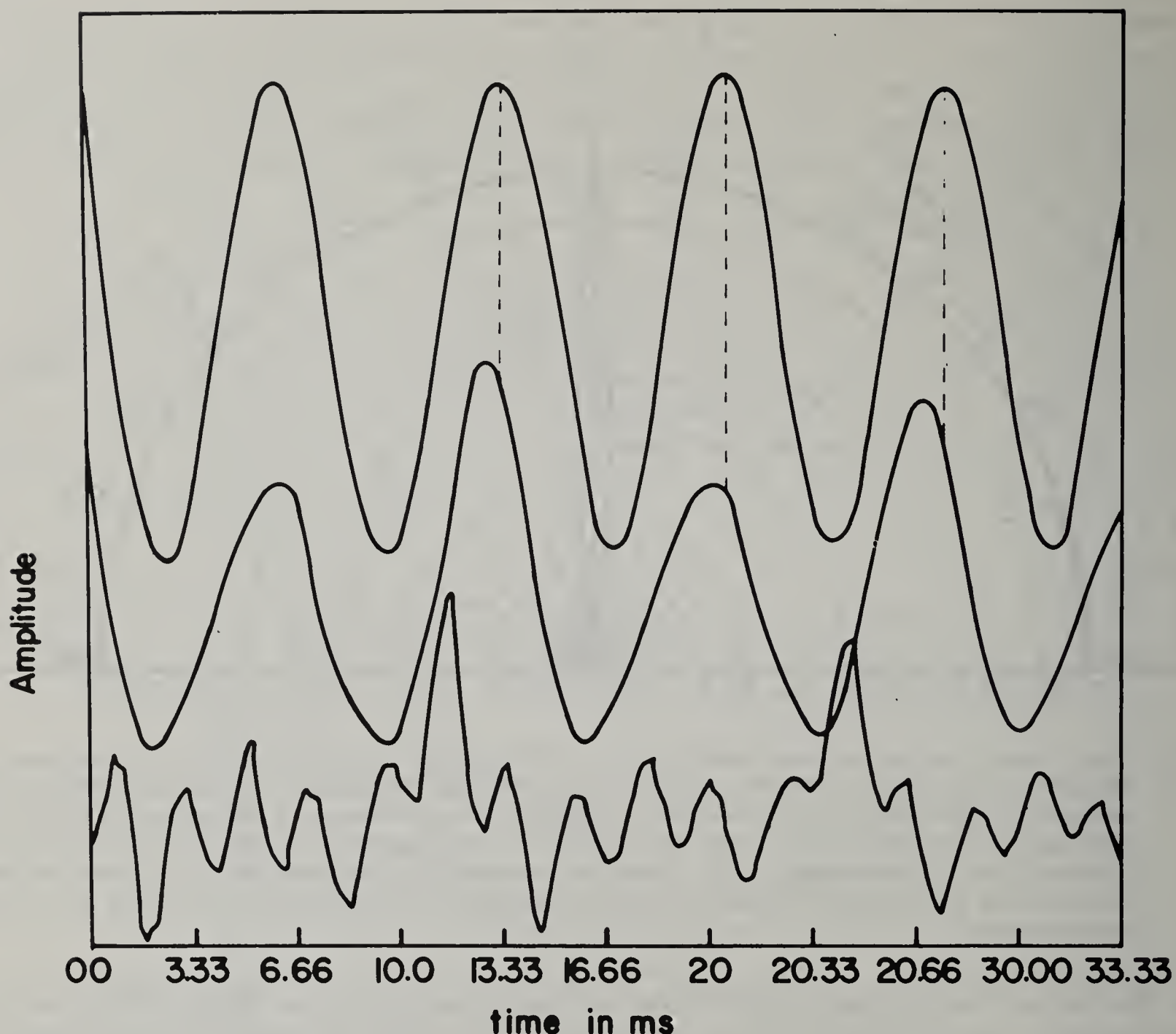


Fig. 23. — Shape of ventilation work of *V. orientalis* workers at nest entrance. The noise produced by wing fanning as recorded and analyzed with an auto-correlator. The amplitude of the auto-correlator is plotted versus time. The top curve shows a repetition rate of 150 times per second. The middle curve was taken six minutes later and it shows a faster repetition rate and smaller amplitude of the up-stroke. In the bottom curve taken six minutes later, the two strokes were split into three shorter swings. It took three minutes of integration to obtain each curve.

of $a_0^{ave} = 15\%$. Above 1600 Hz a_0 is remarkably increased, reaching a maximal value of 95% at about 3150 Hz. The second curve corresponds to an air-space of $d_A = 5.0\text{cm}$. Here the peak-value $a_{50} = 90\%$ already at $fm = 500\text{ Hz}$ and its second, equally high value at $fm = 3150\text{ Hz}$.

As can be seen from Fig. 25, the curve of the larval (workers) hunger signal is, as mentioned earlier, unimodal at 25-2500 Hz and decreases rapidly until 1350 Hz where it is not different from the background noise. If all the noises produced by hornets (*V. orientalis*) are superposed, they invariably decline rapidly and are absorbed in the background noise at 1000 to 1600 Hz. This pattern of the composite curve of hornet noise is visualized as the *reciprocal* of the absorption coefficient curve of the comb. The latter at a_{50} would not enable efficient transmission of sounds whose frequencies exceed 250 Hz. However, the connecting columns between the natural combs are so dense and the distances between them are so small that we can without doubt explain the acoustical properties of the *V. orientalis* comb on the basis of a sound absorption coefficient of a_0 , i.e., as if the combs were a single whole. Figure 26 represents the sound pressure level dB(lin) of *V. orientalis* queen larvae, as a function of a 1/3 octave band. The main sound-energy is concentrated at 80 to 630 Hz, decreasing to very small levels beyond this range. It is obvious that the sounds produced by worker larvae are different than those produced by queen larvae at least with respect to their frequency distribution, and to the absorption properties of the comb. Additional data on the absorption values of various combs at a_0 and at a_{50} are given in Table II, where for purposes of comparison, the combs of *Polistes humilis* and of *Apis mellifera* (males and workers) have also been included.

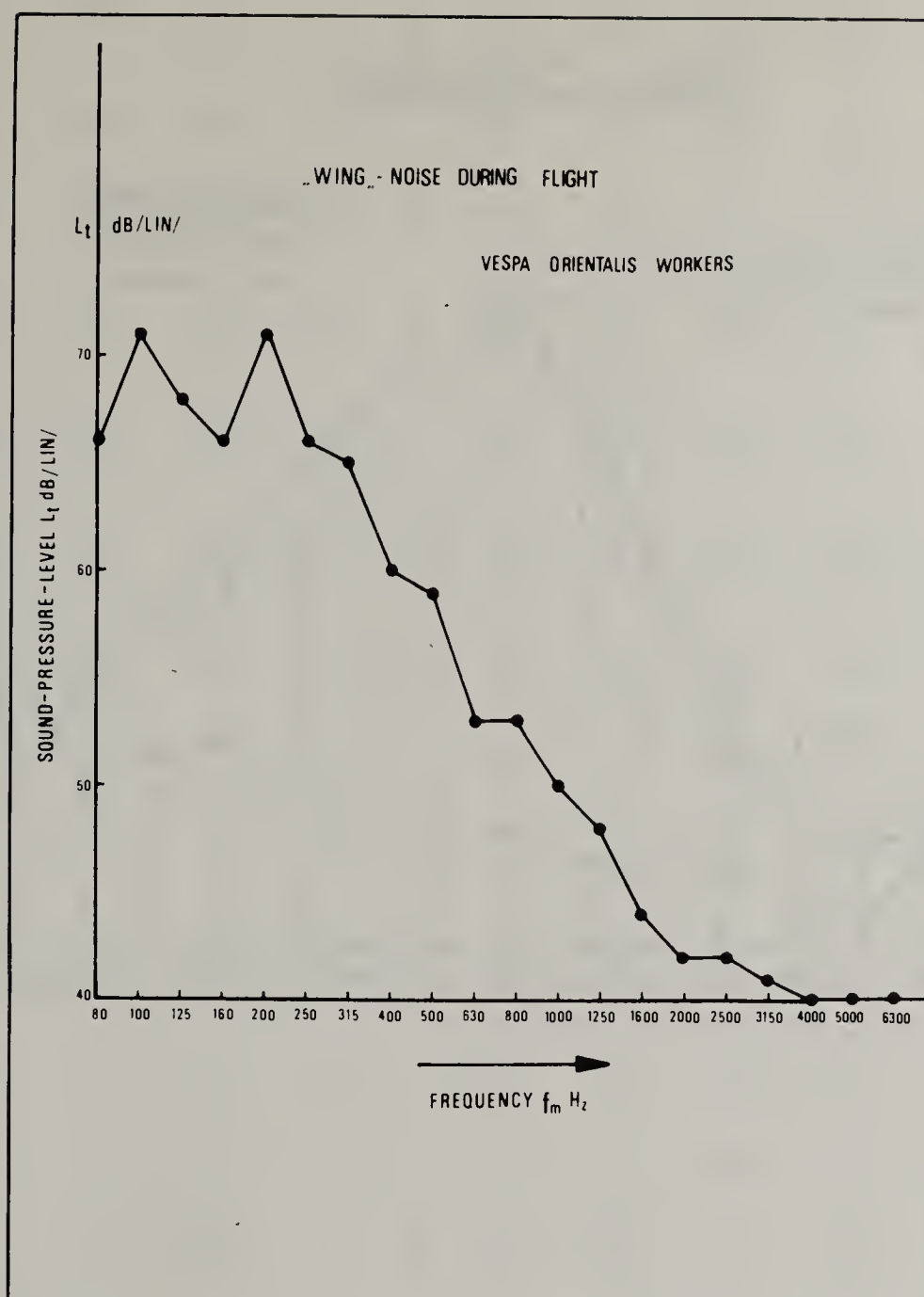
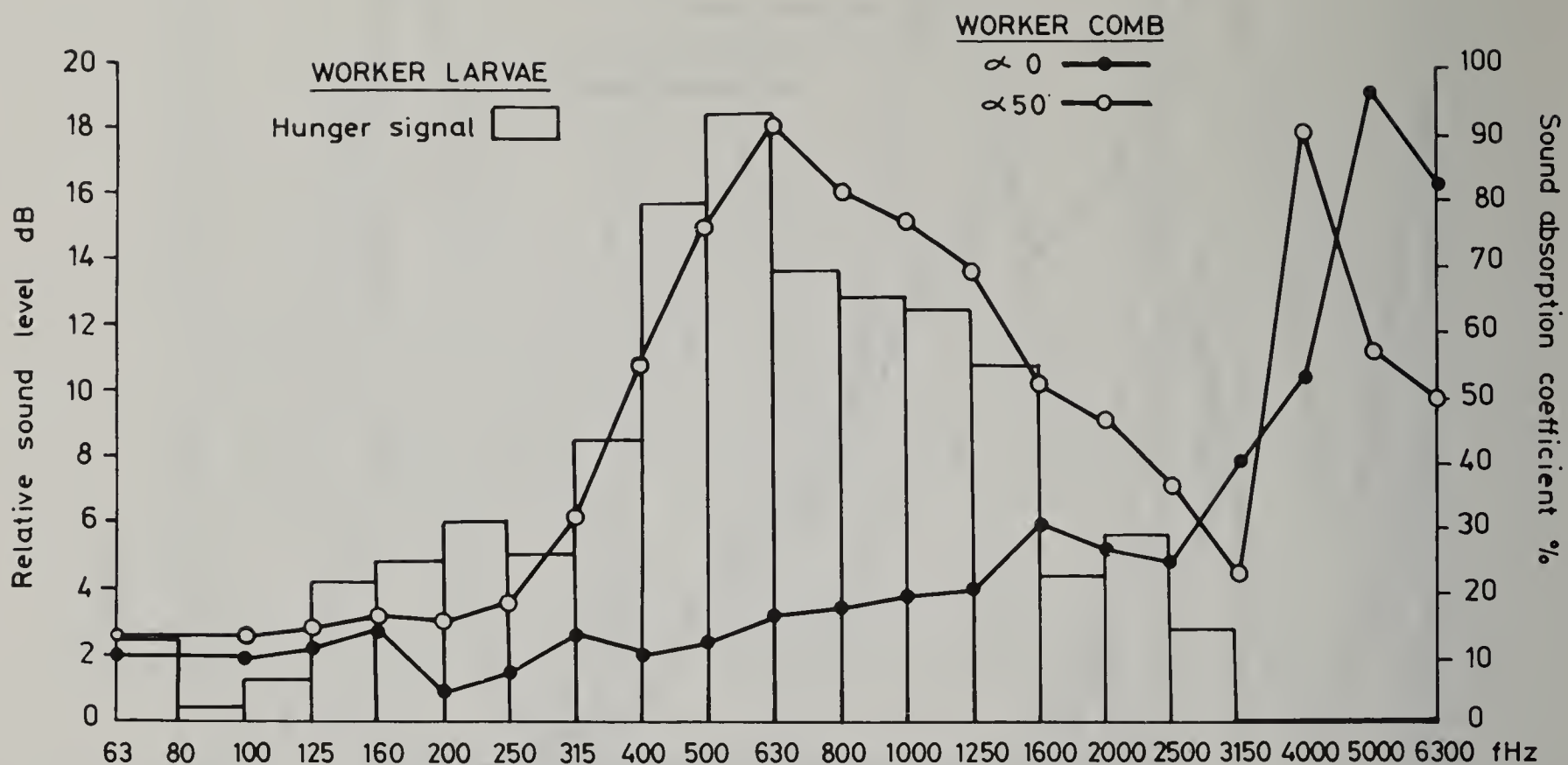


Fig. 24. – The 1/3 octave band sound pressure level $L \times \text{dB}(\text{lin})$ caused by the flight noise of *V. orientalis* workers, as a function of the standard 1/3 octave band frequencies.

The graphic representation for a_0 is shown in Fig. 27 and for a_{50} in Fig. 28. As shown in these figures: (1) the curves of sound absorption co-efficient have a peak on high frequencies, and (2) most of the Vespinae combs have a very similar pattern of absorption values, unlike those of the honeybees. In an attempt to explain its pattern of absorption values, the Vespinae comb may be conveniently visualized as representing a group of Helmholtz resonators. For this purpose, we replace a section of the hexagonal cell by an equivalent circle with an equal area. All the dimensions of a cell in the comb are statistically distributed and fluctuate near their mean values, which are used to estimate the resonance frequency of a Helmholtz resonator: $fR = \frac{C}{2\pi} \sqrt{\frac{2r}{V}}$ where R = resonance, C = sound velocity in air, r = radius of the cell neck, V = volume of the cell cavity. In *V. orientalis* combs as in Vespinae in general, queen cells are bigger than worker cells. The maximal diameter of the cell aperture is 12-13 mm for queen cells versus 8-9 mm for worker cells, and the volume of queen cells is approximately 2 ml versus the 1 ml of worker cells. The resonance calculated value for queen cells is $fR_{\text{queens}} = 3.5 \times 10^3$ Hz and for worker cells $fR_{\text{workers}} = 6.0 \times 10^3$ Hz. As can be seen, there is good agreement between the measured values and the calculated ones. Since the queen cells are bigger, their resonance frequencies are lower. This holds true also for the combs of other species of wasps tested.

Honeybee combs differ from wasp combs with respect to the sound absorption values. Thus, the worker bee comb has high absorption coefficient values at low frequencies (about 100 Hz) and low values at high frequencies (at above 5000 Hz). Male combs have low absorption values at frequencies up to 500 Hz and high absorption values beyond 500 Hz. Generalizing the picture it seems that the absorption values are low both at low and very high frequencies, suggesting that the sounds produced within honeybee colonies are similarly of a low or very high frequency.

VESPA ORIENTALIS



VESPA ORIENTALIS

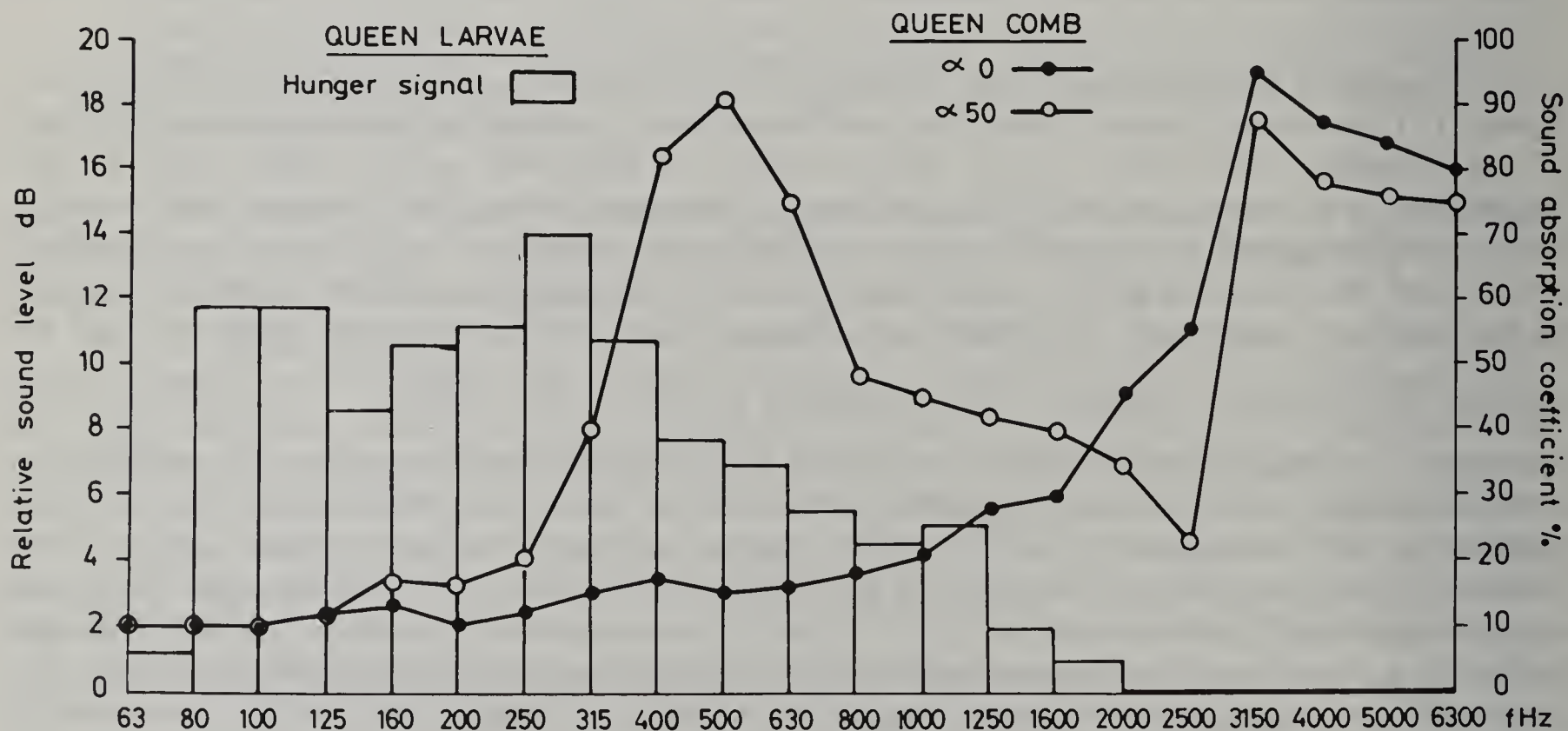


Fig. 25. — The superposition of (a) the frequency dependence of the sound absorption coefficient of the *V. orientalis* worker comb at α_0 and α_{50} and (b) the spectral analysis of 1/3 octave bands of the hunger signal of *V. orientalis* worker larvae. The sound energy is concentrated in the frequency range of 63-1250 Hz. In that area, the absorption coefficient values α_0 are low. The increasing of α_0 and decreasing of the signal begins on about $f=1250$ Hz.

Table 2.—Sound Absorption Coefficient (α)%.

Mean frequency of 1/3 octave band (Hz)		100	125	160	200	250	315	400	500	630	800	1000	1250	1600	2000	2500	3150	4000	5000	6300	8000
Species	Caste	cell vol.																			
α_0	Paravespula germanica	workers	0.2ml	6	6	6	6	6	5	6	14	15	15	17	27	42	52	65	86	82	72
α_{50}	Paravespula germanica	workers	0.2ml	6	6	7	9	9	10	12	20	32	44	63	57	45	34	90	74	55	46
α_0	Paravespula germanica	queen	0.4ml	5	5	5	6	5	5	8	14	14	15	20	28	45	55	80	84	90	70
α_{50}	Paravespula germanica	queen	0.4ml	5	7	7	9	10	16	27	46	75	85	90	67	42	50	80	65	46	42
α_0	P. vulgaris	worker	0.2ml	9	9	8	9	7	8	10	12	14	16	25	34	37	50	74	82	81	79
α_{50}	P. vulgaris	worker	0.2ml	6	6	6	7	6	9	12	20	32	53	57	46	33	73	56	52	70	68
α_0	Dolichovespula saxonica	worker	0.2ml	9	9	9	10	8	8	12	6	17	18	27	31	40	74	83	86	94	84
α_{50}	Dolichovespula saxonica	worker	0.2ml	7	9	12	13	16	19	29	53	67	64	67	53	34	46	85	55	84	55
α_0	Polistes humilis	worker	0.2ml	5	5	5	6	4	7	8	6	10	18	20	30	54	98	78	81	96	60
α_{50}	Polistes humilis	worker	0.2ml	5	6	7	8	8	11	19	35	53	78	75	50	45	65	73	65	65	63
α_0	Vespa orientalis	worker	1.0ml	10	11	14	4	7	13	10	12	16	17	19	20	24	38	90	56	50	44
α_{50}	Vespa orientalis	worker	1.0ml	12	15	16	15	17	30	53	75	90	80	76	46	35	22	90	55	50	44
α_0	Vespa orientalis	queen	2.0ml	10	12	13	10	12	15	17	15	16	18	21	28	55	95	86	84	80	76
α_{50}	Vespa orientalis	queen	2.0ml	10	12	16	15	20	40	82	90	75	48	45	35	22	87	78	75	73	68

a_0	V. crabro	worker	1.0ml	5	6	6	7	6	4	8	8	20	21	25	48	68	75	97	78	80	81	72	68
a_{50}	V. crabro	worker	1.0ml	6	7	10	10	10	12	25	50	65	70	52	47	39	40	40	60	75	75	73	65
a_0	Apis mellifera	worker	0.2ml	30	20	87	8	70	45	67	60	50	66	56	62	46	32	22	28	27	22	15	12
a_{50}	Apis mellifera	worker	0.2ml	12	70	28	35	40	80	92	85	50	60	48	65	27	32	22	26	27	22	16	11
a_0	Apis mellifera	male	0.4ml	6	5	3	4	6	9	13	20	58	30	56	57	45	75	84	68	73	40	32	27
a_{50}	Apis mellifera	male	0.4ml	7	8	14	23	35	62	90	85	75	55	36	32	24	27	22	24	24	55	50	45

α_0 - The sample is placed at zero distance from the closed side of the standing-waves tube.

α_{50} - The sample is placed 50 mm from the closed side of the standing-waves tube.

- 1 - APIS MELLIFERA (worker comb)
- 2 - APIS MELLIFERA (male comb)
- 3 - VESPA CRABRO (worker comb)
- 4 - DOLICHOVESPUA SAXONICA (worker comb)
- 5 - POLISTES HUMILIS
- 6 - PARAVESPUA VULGARIS (worker comb)
- 7 - PARAVESPUA GERMANICA (queen comb)
- 8 - PARAVESPUA GERMANICA (worker comb)

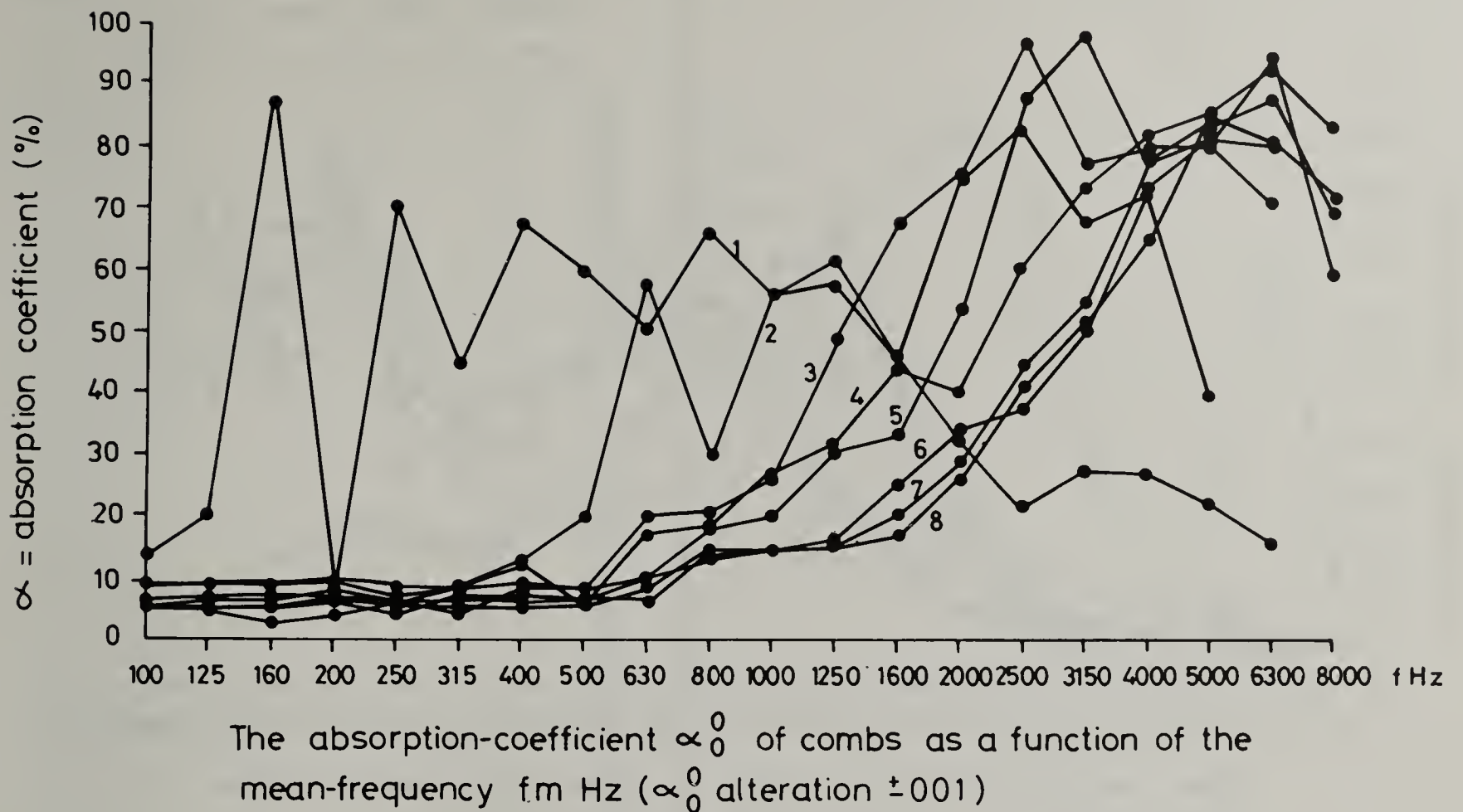


Fig. 26. – Same superposition as in Fig. 25 but with a queen larval comb and queen larval hunger signal. The sound energy is concentrated in frequency range of 80 to about 800 Hz. There is a decreasing of related sound level from $f=400$ Hz to $f=1600$ Hz.

Interestingly, it was found by Hansson (1945) that the average frequency of 'piping' [which according to Simpson and Cherry (1969) induce swarming] is 435-493 Hz, while for 'quacking' sounds it is 323 Hz. On the other hand, Wenner (1962) reported higher values for the same sounds: 1300 Hz for piping tones and 2500 Hz for quacking tones. Both authors are probably correct, for the discrepancy stems from the varying absorption values of the bee comb.

Bearing in mind the aforementioned comb resonance values, then the changes which hornets and wasps make in combs that differ from their own assume a new perspective. It will be remembered that hornets narrow the outlet of the wide-mouth cells (Fig. 10), and that this is probably sufficient to enable worker larvae to develop in queen cells. In fact, the hornets are merely altering the diameter of the neck of the classical Helmholtz resonator but they probably are aware of it! Wasps, on the other hand, are apparently sensitive also to excess cell volume, because when presented with cells more than twice as large as normal, they build intrapartitions (Fig. 9) that render the cells smaller, so it seems that they are not only sensitive to neck dimensions, but also to volume per se, within certain limits.

Perhaps adult wasps and hornets 'understand' the sounds produced by the hungry larvae as messages conveying data on their caste, age, degree of hunger, etc. It should be remembered, however, that when feeding the larvae, the adults receive in return droplets of larval saliva. This larval saliva is rich in nutrients and contains a high level of glucose (Table 3). The glucose content of the saliva is different at the various castes and ages (Fig. 29) and drops slowly during starvation so that it could possibly provide additional information on the larva beyond that already provided in its sounds. In any case, it is quite likely that in Vespinae, acoustic communication is employed to convey information about conditions within the nest.

- 1 - PARAVESPULA GERMANICA (queen comb)
- 2 - POLISTES HUMILIS
- 3 - DOLICHOVESPULA SAXONICA (worker comb)
- 4 - PARAVESPULA GERMANICA (worker comb)
- 5 - APIS MELLIFERA (worker comb)
- 6 - PARAVESPULA VULGARIS (worker comb)
- 7 - VESPA CRABRO (worker comb)
- 8 - APIS MELLIFERA (male comb)

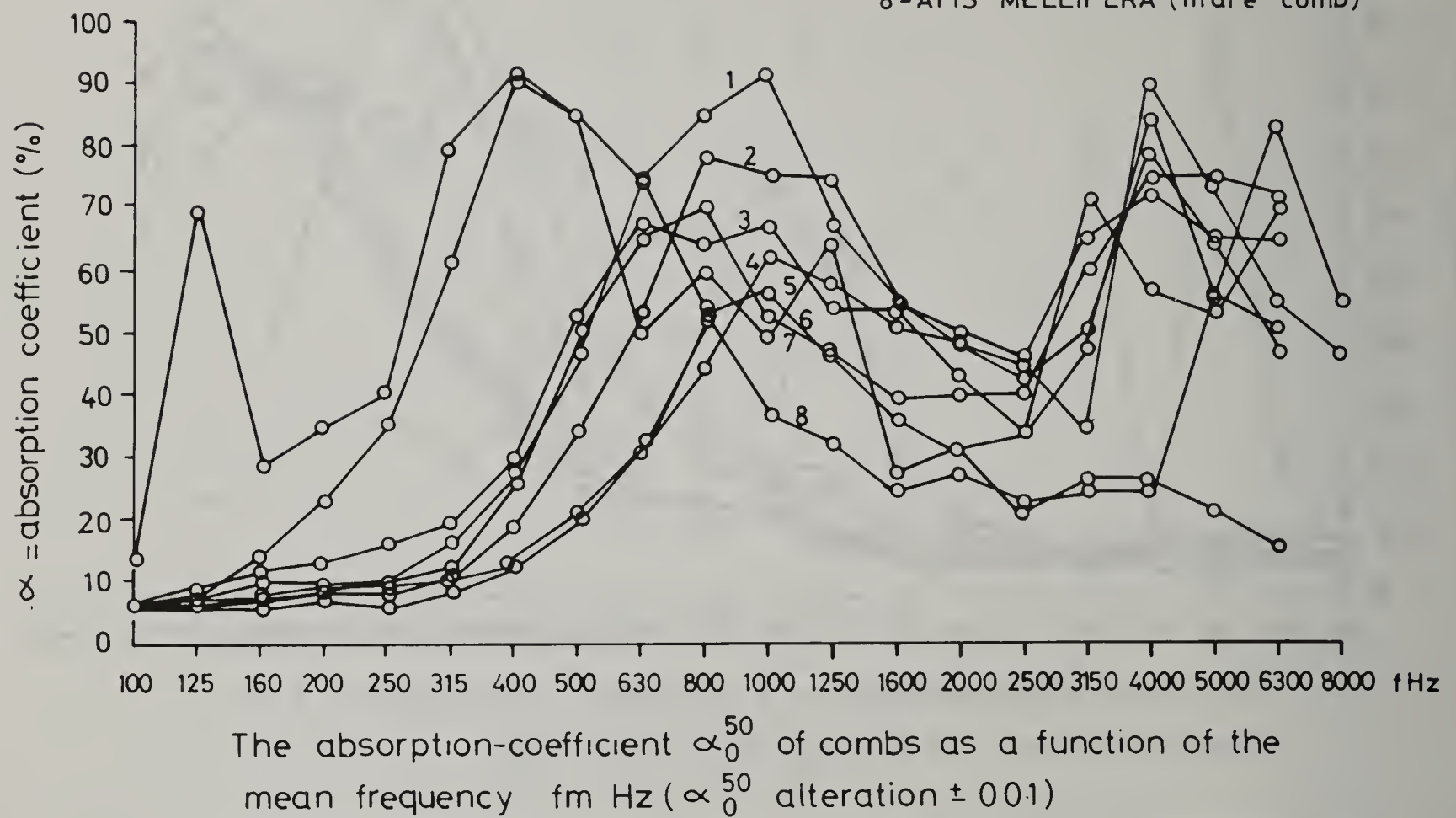


Fig. 27. — The absorption coefficient α_0 of various Vespinae combs and for comparison purposes also of *Polistes humilis* and of *Apis mellifera* worker and male comb. The values for Vespinae combs are quite low and constant in frequency range of 100-630 Hz where most probably the sound energy of the communicative signals is concentrated. Note that the values of *Apis mellifera* combs are different than those of Vespinae.

What happens in Larva-less Nests, i.e., in a Nest Whose Combs Are Devoid of Brood?

In the presence of an ovipositing queen, the workers retain an attachment for the combs, i.e., they guard the laid eggs and nurse the hatched brood. There is thus constant activity in the comb whose purpose is both to maintain optimal conditions for the developing brood as well as to provide and distribute food for the various members of the colony. However, when there is no brood in the comb cells, the nest is abandoned, for the workers do not remain in a nest or on combs which are broodless and in which the larval hunger signals are not sounded.

Are the specific sounds produced by the larvae and adults acquired through learning or possibly through a process of mimicry (of their own or other species)?

In view of the fact that the colony is formed anew itself every spring, it is rather unlikely that the initial larvae *learn* to produce their hunger signal. It is more reasonable to assume that they produce the hunger signal spontaneously. However, as the brood increases in the course of the season, the larval hunger signals within a particular comb tend to become synchronized. It would seem, therefore, that while the hunger signal itself is a spontaneous, unlearned behaviour, its synchronization into the generalized signal pattern of all the larvae is something that is learned in the course of larval ontogeny. Are these sounds species specific? There can be little doubt that the larvae of each wasp species produce their own specific hunger signal. We have shown that the larval hunger signal has a specific acoustic spectrum which is dependent both on the activity rhythm of the larvae as well as on the absorption coefficient of the comb, or by way of a musical analogy — on the acoustic qualities of the 'player' (the larva) on the one hand, and on the physical qualities of the 'musical instrument' (the comb) on the other. And yet, despite the disparity between wasp species, it is clear to anyone

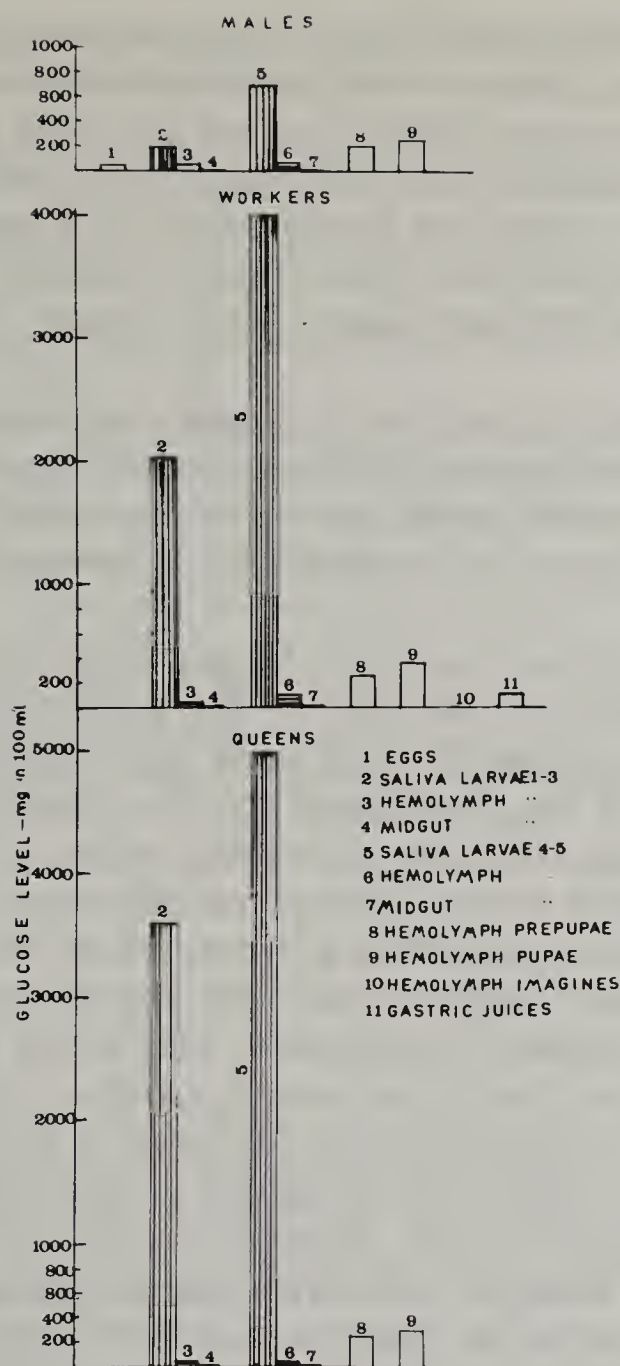


Fig. 28. – The absorption coefficient α_{50} for combs as in Fig. 27. The absorption coefficient values are low at 100-250 Hz and start increasing afterwards.

VESPA ORIENTALIS
GENERAL CHARACTERISTIC AND CONTENTS OF LARVAL SALIVA COMPARED WITH OTHER BODY FLUIDS

PROPERTIES MATERIAL		PHYSICAL PROPERTIES					ORGANIC CONTENTS					E N Z Y M E S				L.M.W. PHARMACOLL. SUBSTANCES								MISCELLANEOUS		
		pH	OSMOLALITY mil. osm/kg	Na mEq/L	K	Cl	T O T A L			URIC ACID mg %	FREE AMINO ACIDS	PROTEOLYTIC		CHOLINESTER	HYALURONID.	KININ LIKE	EPINEPH 7/8	NOREPI 7/8	DOPA 7/8m	5-HT 7/8m	ACH	HISTAMINE	ELECTROPHORETIC MIGRATION Fr No	ANTIGENIC FACTORS	MICRO - FLORA	
							PROTEIN gm%	GLUCOSE mg%	LIPIDS gm%			ENDO	EXO													
L A R V A E	SALIVA	4.5-6.6	460-657	26	19.2	6	1.4	2840-3500	2.8	14.5	+	±	+	+	-	+	1.18	2.21	7.10	1.43	-	-	BASIC PROTEINS 1,4,6,8,11	1	STERILE	
	HEMOLYMPH	5.6-6.8	385-560	37.6	21.0	30	7.8	212	3.8	7.5	+	-	-	+	-	-	0.65	0.84	2.08	0.60	-	38/ml	1,4,7,8	6	STERILE	
	MID - GUT	5.5	520-780	6.0	21.2	7.0	3.64	40- 50	9.2	13.0	+	+	+	+	-	FACTORE PROB. HISTA. FACTOR J	164	2.54	22.58	2.17	-	+	BASIC PROTEINS 1,8,11	2	B. PROTEUS COLLIFORM BACCILI	
A D U L T S	GASTRIC JUICE	4.85-6.0	280-495	24	270	32	7.3-7.6	1008-2660	2.2	18.5	+	-	-	+	-	+	WORKERS 0.44 1.56 3.52 4.00 + QUEENS IN SPRING				-	-	1,2,4,8	1	B. PROTEUS C. BAC. ST. AUR.	
																	0.44	0.91	1.98	0.13	+					
	VENOM	5.5-6.5						20.5	+	+		+	+	±	-	+	!	48	58	128	736	+	+	BASIC PROTEINS 1,7,8,9,12	4	STERILE
METHODS		pH-METER GLASS ELECT.	ADVANCED OSMOMETER	FLAME PHOTOMETRY	CHLORIDO - METER	TECHNICON AUTO - ANALYSER	ANTHRON TECHNICON AUTO - ANAL.	GAS-CHROM. ETHER EXTR.	TECHNICON AUTO-ANAL.	PAPER ELECTROPHOR.	GEL FILM DIGEST. ATEE (CHYMO) TAME (TRY)	HPLA, HPA, HA.	ELLMAN METHOD	TURBIDITY	GUINEA PIG ILEUM RAT UTERUS	ADRENOLU-TININE	RAT UTERUS SPECTROPHOTO-FLUORIMETER	FROG RECTUS	G. PIG ILEUM	250V, 20' STAINING NEGROSIN 3% SULPHO SALICYLIC ACID	OUCHTER LONY'S TECHNIQUE RABBIT ANTISER.	AGAR BLOOD DISHES				

Fig. 29. – Glucose levels in various tissue fluids of *Vespa orientalis*.

who has investigated Vespinae that all adult wasps recognize the hunger signals of their own larvae as well as of those of other species, although they are definitely more partial to the hunger signals produced by their own larvae. Montagner (1964) reported that when a wasp comb containing larvae is left on the ground outside the original nest, adult wasps settle on it and start nursing the larvae. During the first day, only a few adults land on the comb but subsequently their number increases daily until a certain maximum is reached and a new colony is formed. Montagner called such colony a parasocial one and believed that the adult wasps were initially drawn to the comb by sounds produced by the larvae.

There are many observations of usurpation or adoption of another colony by queens or workers of the same and different species. Desey (1922) has observed that queens of *P. germanica* and *D. sylvestris* adopted nests of their own species as long as they contained viable larvae. On the other hand, Nixon (1936) noted that queens of *P. vulgaris* and *P. germanica* may adopt nests of their own or the other species.

We have noted that as the larvae sound their hunger signal, the workers rush to 'silence' them through feeding. Why this urgency on the part of the workers? Possibly we are dealing with a protective reflex, the rationale being that the larval noise may inadvertently reveal the location of the nest to nearby predators and that the adults must therefore silence the larvae to protect the nest. Again, by analogy, the wasp larvae are thus comparable to the young of mammals whose crying prompts their mothers to stuff their mouths with an available nipple to prevent any give-away noise.

The goslings of nesting birds are known to lift their heads and open their beaks in demand for food only when one of the parents alights on the nest — in other words, a mechanical stimulus is necessary to trigger the hunger response. In the case of wasp larvae, a mechanical stimulus may elicit the hunger signal, but this is also produced spontaneously, without any external stimulus.

It is interesting to note that the absorption coefficient of the comb at α_0 is different than at α_{50} . From all our measurements, it seems that absorption of sounds occurs primarily at α_0 , i.e., when the combs are interconnected or juxtaposed. When the combs are not interconnected, i.e., at α_{50} , there is a high measure of sound absorption already at the low frequencies. From the standpoint of the acoustic spectrum of the wasp sounds, there is correlation mainly with the absorption coefficient obtained at α_0 . It thus seems that in the cases studied by us, the comb structure and the acoustic communication conformed to that of wasps of the stelocytтарous group, who build combs which are centrally and peripherally interconnected by means of pedicles. On the other hand, the absorption coefficient obtained at α_{50} conforms to that of phragmocytтарous wasps whose combs are interconnected only at the margins, leaving relatively large portions of the combs unconnected.

Both the larval and adult sounds are produced as solid-borne sounds, but they are transmitted from comb to comb or to the surrounding nest ambience as air-borne sounds. It is yet to be determined whether the wasps are capable of hearing airborne sounds.

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Egg Laying, Aggression and Dominance in Bees

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ABSTRACT

After mentioning the possible modes of action of honey bee queen pheromones the multiple functions of the queen substances are discussed. These functions converge in the recognition by means of chemoperception. The several reactions of the workers towards presence or absence of the queen are the result of complicated regulatory mechanisms inside the worker rather than a multitude of isolated effects of the queen on her workers.

Such a situation might have been evolved from the introduction of a chemical signal to supplement overt aggression in the social evolution. For the honey bee the sex pheromone of the queen might have served for this purpose. Comparisons with stingless bees and with laying worker colonies support the idea that the queen pheromones are to be considered as signals in behavioural interactions.

In this paper I will discuss the influence of the queen of social bees on the behaviour of her worker bees and on the functioning of their ovaries. This kind of interrelationship is mainly studied in the honey bee and that animal will get the most emphasis. Comparisons with both laying worker colonies and Stingless Bees result in the speculation that queen pheromones are signals in behavioural interactions. The dual function of these signals seems to be to increase the brood production without the queen losing control over the reproduction of the workers and at the same time providing a substitute for overt aggression.

By no means this speculation will be proven here.

Honey Bee Queen Pheromones: The Mode of Action

In the honey bee colony the queen produces a number of pheromones to regulate the activities and the related physiological conditions of the workers. Far more pheromones are postulated than are chemically known (Table 1). Only two pure substances from the mandibular gland of the queen, the 9-oxo-trans-2-decenoic acid and the 9-hydroxy-trans-2-decenoic acid have been tested for their biological effects.

Since the introduction of the term 'queen substance' by Butler (1954) there has been difference in opinion on the mode of action of the substances. Some effects of the queen, for instance her inhibiting effect on the ovarian activity of the worker, have been attributed by some authors to a direct chemical-hormonal effect; these substances therefore are considered to reach in some way the interior of the worker. In contradistinction, others believe such effects are the result of chemoperception, that is of chemical communication, between queen and worker followed by subsequent hormonal adjustments in the latter. The two extremes are put in scheme in Fig. 1.

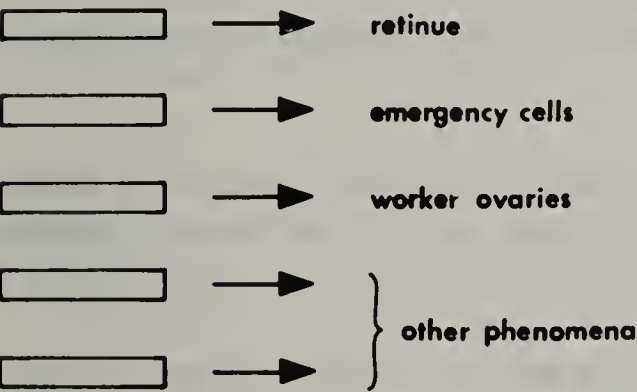
This discussion is well known and I will not go into the older literature, but will refer the reader to the papers by Butler (1954, 1969, 1973), van Erp (1960), Johnston, Law and Weaver (1965), Verheijen-Voogd (1959) and Velthuis (1970a, 1972).

Table 1.—Some Known and Postulated Pheromones of the Queen.

Pheromone	Source	Effect on	Author(s)
9-oxo-decenoic acid	Mandibular gland	Worker and drone behaviour, worker physiology	Barbier et al. (1960) Butler et al. (1962)
9-hydroxy-decenoic acid	Mandibular gland	Worker behaviour and physiology	Butler et al. (1964)
unknown	Dorsal abdominal glands	Worker behaviour and physiology inside hive	Velthuis (1967, 1970)
unknown	Dermal glands	Worker attraction inside hive	Butler (1954, 1963)
unknown	Koschewnikow gland	Worker attraction during swarming	Butler and Simpson (1965)
unknown	unknown	Discrimination between virgin and mated queen by workers inside hive	Butler (1954)
unknown	unknown	Discrimination between own and foreign queen	Velthuis and van Es (1964) Morse and Boch (1971), Morse (1972)
Stress pheromone	Mandibular gland	Worker behaviour towards queen	Yadava and Smith (1971)
unknown	Mandibular gland?	Synergist of sex pheromone, 9-oxo-decenoic acid	Gary (1962) Pain and Ruttner (1963)
unknown	Mandibular gland	General synergist of 9-oxo-decenoic acid	Pain (1961)

PHEROMONES ACT INDEPENDENTLY

(through sense organs and/or biochemical)



PHEROMONES ACT THROUGH A COMMON MECHANISM

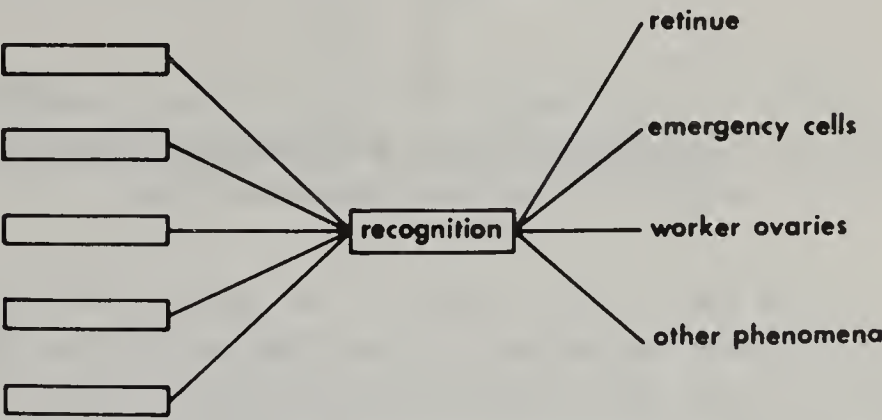


Fig. 1. — The two opposed modes of action of the queen pheromone complex.

Some Experiments

Some of our experiments that are partly published in Velthuis (1971) compare the effects of different pheromones or different mixtures on the two most extreme releasers, resp. most extreme

primer aspects (Wilson and Bossert, 1963), of the queen substance that is the retinue behaviour and the final ovarian state of the worker. According to the two models presented in Fig. 1, after the separation of the various constituents of the complex 'queen substance' we either will find a segregation of the releaser and the primer effect, or these two are linked and can only be altered in a quantitative sense, depending on the degree of 'recognition', thus depending on different concentrations. Such a relation with concentration indeed exists (Fig. 2). A similar graph resulted when only the chemical pure 9-oxo-decenoic acid was given.¹ Apparently, this substance, like the abdominal factor, affects both characteristics (Fig. 3).

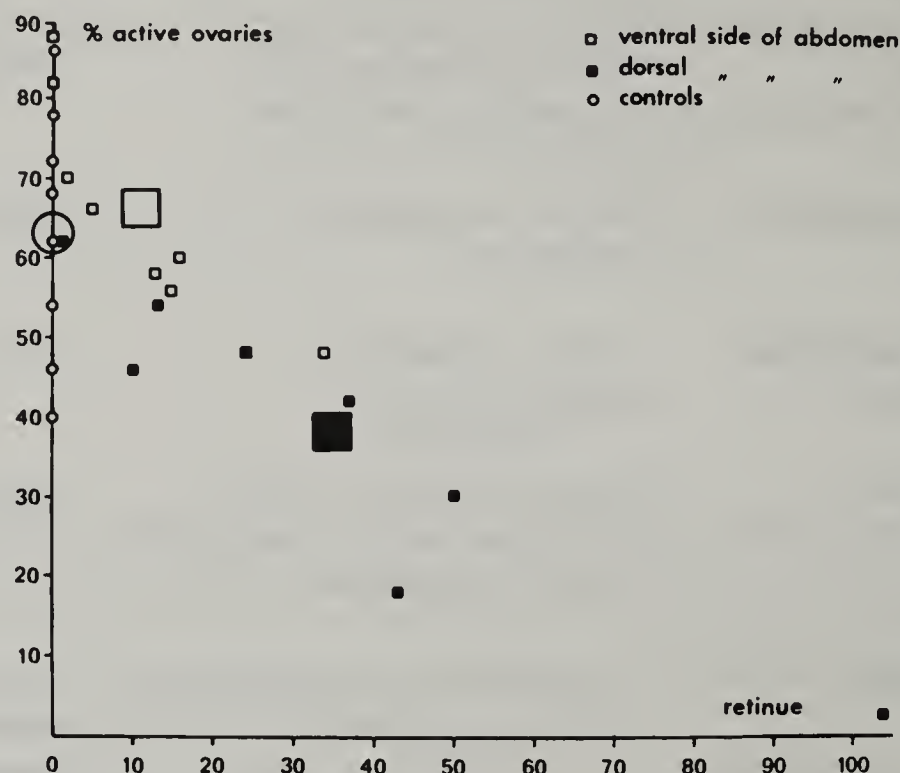


Fig. 2. – The correlation of the effects on retinue behaviour and ovarian activity of worker honey bees when isolated abdomina of queens without mandibular glands were present in their cages.

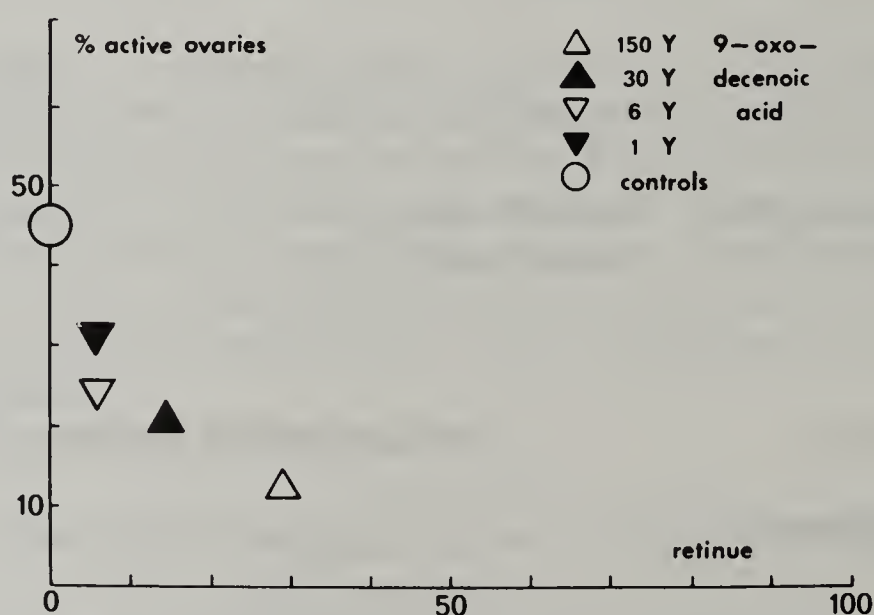


Fig. 3. – The relation between retinue behaviour and ovarian activity when different quantities of 9-oxo-decenoic acid were present on a dead worker bee.

In Fig. 4 the effects of an acetone extract of intact queens, probably containing several pheromones and at least the two fatty acids from the mandibular glands, and the abdomens of queens free of these two acids are compared. Here there is no reason to conclude that different modalities in our different representations of the factor 'queen' exist.

In the last experiment in this series both the 9-oxo-decenoic acid and the 9-hydroxy-decenoic acid were given and compared with the glands that produce these substances (Fig. 5). A similar negative correlation between retinue and ovary activity was found, irrespective of the two substances being separately given or in a mixture. Again, no different modalities appear.

¹The pure 9-oxo-decenoic and 9-hydroxy-decenoic acids were obtained from Dr. Boch, Ottawa, and Prof. Arens, Utrecht.

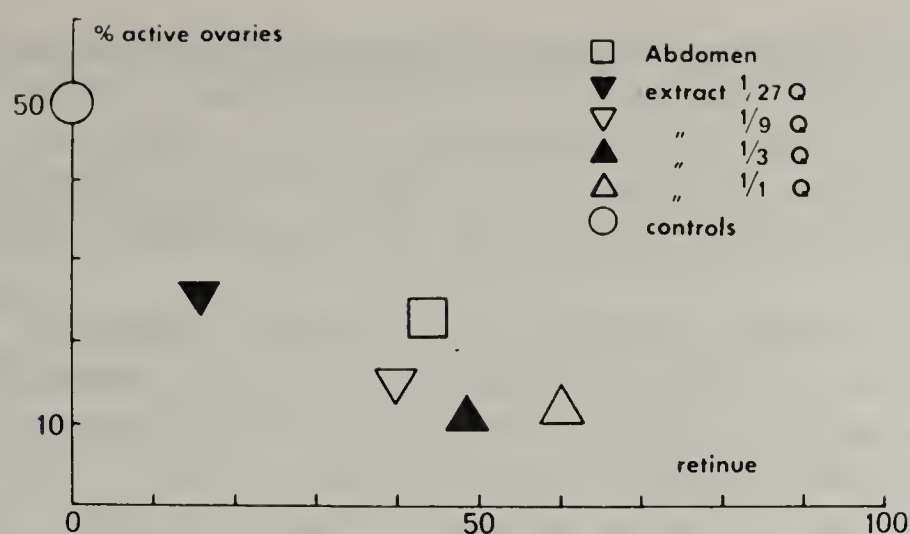


Fig. 4. – The correlation between retinue behaviour and ovarian activity when different quantities of a queen extract (Q denotes the quantity obtained from the average queen) or isolated abdomina of queens without mandibular glands were presented.

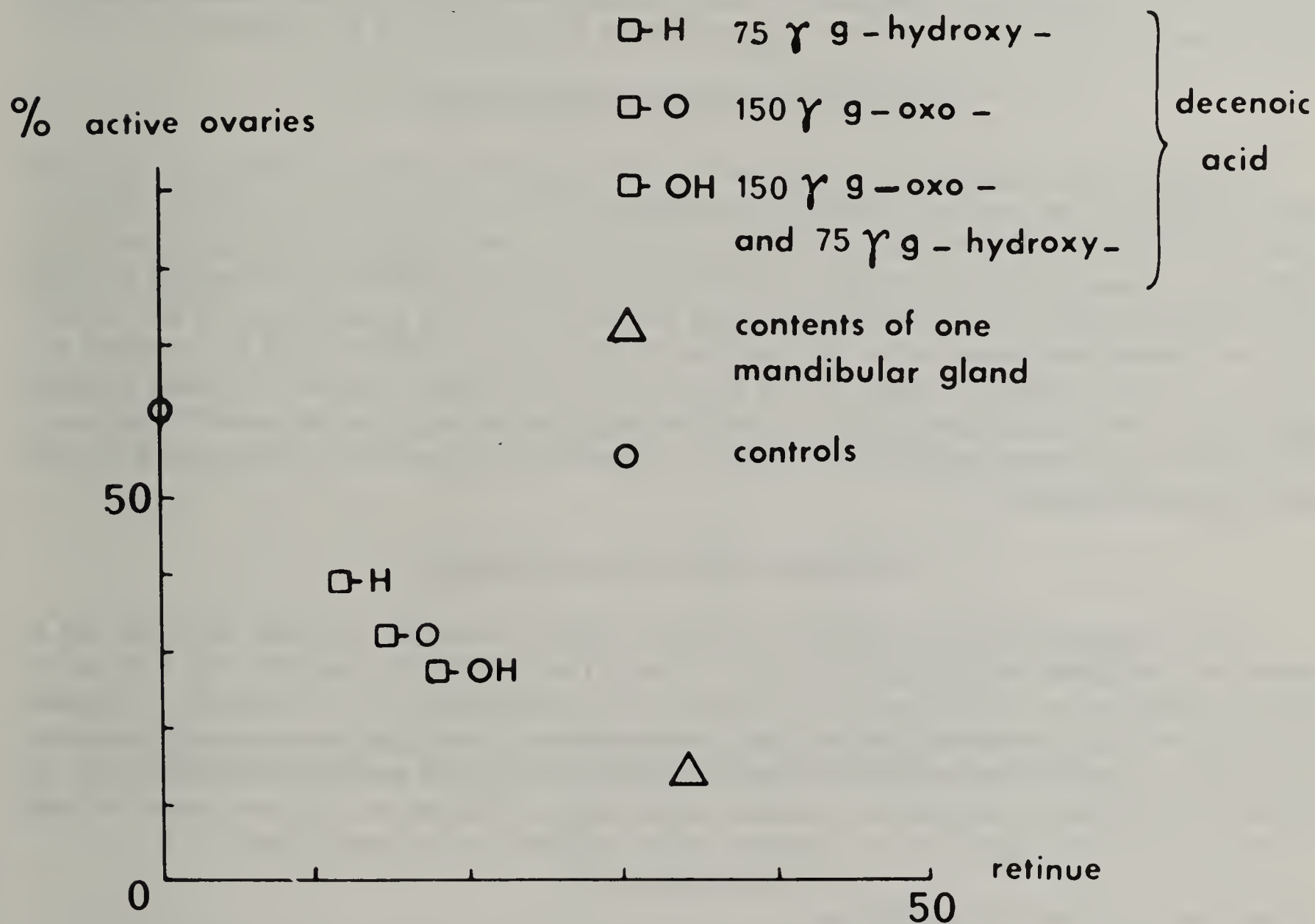


Fig. 5. – The effects of 9-oxodecenoic and/or 9-hydroxydecenoic acid on retinue and ovarian activity of worker bees, in comparison with the effect of the contents of one mandibular gland, having about the same amounts of these substances.

Multiple Functions

At the same time we recognize the multiple effects of the 9-oxo-decenoic acid. The substance is a sex attractant during the nuptial flight of the queen. Gary (1962), Pain and Ruttner (1963), and Strang (1970) concluded that also other attractants are produced by the queen, but Boch et al. (1975) proved that only this factor functions as sex attractant.

This substance also evokes retinue behaviour in worker bees (Velthuis and van Es 1964; Fig. 3 of this paper), prevents them from building emergency cells (Butler, Callow and Johnston, 1962) and from activating their ovaries. Furthermore, it is involved in worker attraction during swarming (Morse and Boch 1971, Boch et al. 1975).

The other substance, 9-hydroxy-decenoic acid, plays no role in the sex attraction (Boch et al. 1975), although Adler et al. (1973) obtained EAG's from drone antennae with this material. To worker bees it can serve to release retinue behaviour (Fig. 5), to inhibit emergency cell construction (Butler and Callow 1968) and to affect the ovaries (Fig. 5). For its role in swarming behaviour Boch et al. (1975) reject the conclusion of Butler et al. (1964) and Butler and Simpson (1967) that is involved in the attraction.

Here I may point to the often confusing use of the word "attraction". Whereas swarming bees move towards the queen, they do not move towards her when in an undisturbed colony (Butler et al. 1973), but form a retinue when they meet her by chance. We might remember the paper by Dethier et al. (1960) which distinguishes between attractant and arrestant. This double function of the substance in the behaviour of the worker toward the queen apparently originates in her central nervous system.

A similar arrestant function possibly has the abdominal pheromone (Velthuis 1970b) for mating. Butler (1971) found that before mounting the queen the drone touches her abdomen with the very tip of his antennae. Kaissling and Renner (1968) however, did not obtain electrophysiological reactions from single cells of the pore plates of drones after stimulation with this odour.

Evolutionary Origin of Queen Pheromones

Probably, when accepting the hypothesis that the worker's reactions to the queen depend on the recognition of her presence through chemoperception, either by odour or by contact, and that subsequent physiological processes are fully governed by her own regulatory mechanisms, we might consider the queen pheromone complex as being derived from an original sex pheromone in which the 9-hydroxy-decenoic acid is a precursor of the sex pheromone. The diversification of the worker's reactions evolved then along with the evolution of caste polymorphism, both in behaviour and anatomy, once the dominant female started to use her sex pheromone along with the more primitive aggression in preventing oviposition by competitive daughters. An insight in the possible evolution of this complicated communication system might be supported by the result of comparisons with some other advanced bee species.

Comparisons with Other *Apis* Species

A first comparison can be made with the three other *Apis* species. Of these, *A. florea* and *A. dorsata* are considered as more primitive than *A. indica* (= *cerana*) and *A. mellifera*. Fig. 6 shows the frequency distributions of the number of ovarioles of the workers along with the number of ovarioles of the queens.² In *A. mellifera* the immature female has in the developing ovary about 70 ovarioles. This number reduces in the worker and increases in the queen and we may take the difference in the numbers of ovarioles in the adults as a measure of the degree of difference of the two castes. In doing so, we can put the four species in the following order: *mellifera*, *indica*, *florea*, *dorsata*.

Laying Worker Colonies of *Apis* Species

When we remove the queen from the colony and prevent queen rearing by the workers, some workers will start laying eggs. In *A. mellifera* many bees will activate the ovaries, but few will become an egg layer. Perepelova (1929) already distinguished between anatomical and functional laying workers. It seems as if the laying workers, just like the queen, do prevent the others to produce eggs (Velthuis et al. 1965, Velthuis, 1970a). In *A. indica*, this capacity seems to be more pronounced and also the workers start egg laying sooner than in *mellifera* (Sakagami 1968). Also much more pronounced seems the appearance of the 'false queen,' a worker evoking retinue behaviour and having a similar behaviour as the normal queen.

Although but few indications exist, in *A. dorsata* perhaps the effect of a laying worker on the ovary of the other workers is more pronounced. Laying worker colonies encountered by Morse and

²The *A. dorsata* and *A. florea* bees were obtained through the kind cooperation of Mr. D.B. Mahindre, Dr. G.B. Deodikar, Prof. Dr. N.C. Pant and Prof. Dr. G.P. Sharma, India. For *A. dorsata* also material collected in the Phillipines by Prof. Dr. R. Morse and Dr. F.M. Laigo was considered.

Laigo (1969) in the field had many eggs and drone brood but rather few workers with active ovaries (Velthuis et al. 1971).

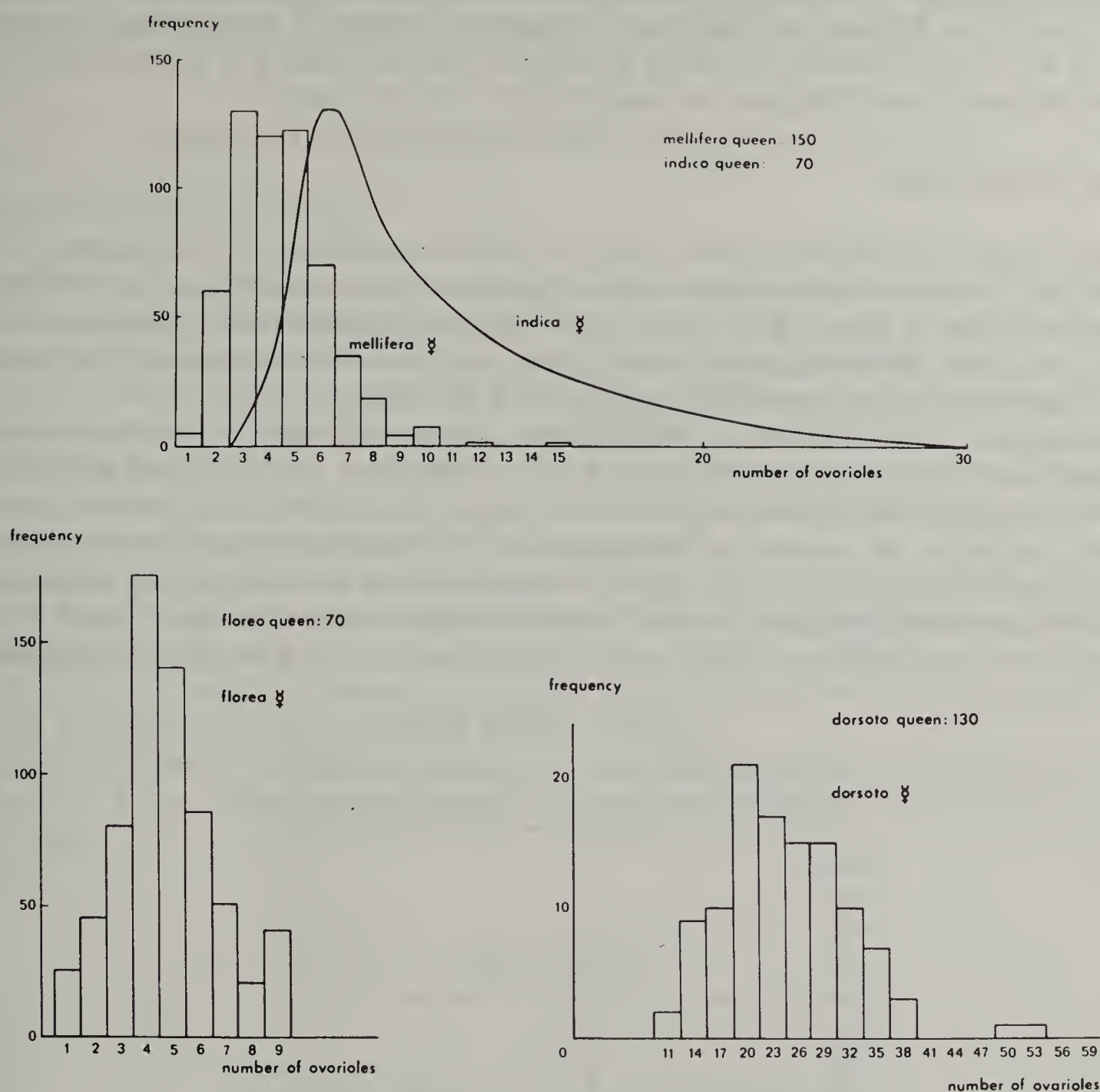


Fig. 6. – The frequency distribution of the number of ovarioles per ovary of the workers of the four *Apis* species. Data on *Apis indica* (= *cerana*) after Sakagami and Akahira (1958) and Kapil (1962).

The Stingless Bees

The closest relatives of the honey bees are the stingless bees. Here in some species, probably the most primitive ones, just like in the honey bee the queen prevents egg laying by the workers at the level of the hormonal control, that is she prevents all stages of oogenesis. In other species, however, the ovaries of the workers fully function. They produce the eggs giving rise to males (Beig 1972). Eggs laid by workers are often consumed by the queen before she deposits her own egg in to the cell. In some species the workers even produce special eggs without a nucleus for this purpose. Of the many excellent papers on this group by Sakagami and Zucchi and their collaborators I mention only a few recent ones: Sakagami, Camilo and Zucchi (1973), and Sakagami and Zucchi (1974).

In restricting ourselves to the genus *Melipona*, we see that oviposition is a process of highly interactive nature. Once a brood cell is built, a number of workers assemble on the comb and wait for the queen to come. After her arrival she starts a complex display, called 'cell fixation' by Sakagami, during which she inspects the cell and produces a signal that releases food deposition by a number of workers into the cell. Strong contractions of the abdomina indicate that the bees empty their honey-stomach into the cell. During this process the queen checks at times the quantity present. After a number of food discharges a worker may deposit an egg, that is eaten by the queen, after which she herself lays an egg and leaves; a worker finishes by closing the cell.

Sakagami, Camilo and Zucchi (1973) point out that a comparison of the oviposition process of the several Meliponid species leads to the tentative conclusion that the regulation of this process is governed by aggression. The queen is socially dominant, which dominance is probably supported by specific pheromones. Removal of the queen immediately blocks all reproduction. Apparently, the triggering of the food deposition by means of a signal from the queen is at the same time the control mechanism the queen uses to regulate the reproduction of her workers.

The Laying Worker Colony

In the normal oviposition process there are several indications for the presence of ritualized aggression. Even more pronounced is the role of aggression once a queenless colony develops into a laying worker colony, a process that like in the honey bee, needs several weeks to occur. We had the opportunity to study this in *Melipona favosa*,³ a bee that can well be compared with the much more studied *M. quadrifasciata* (Sakagami, Montenegro and Kerr 1965).

A description of the behaviour during the cell provisioning and oviposition process of a *M. favosa* laying worker colony is summarized in Fig. 7. After an extended period, during which a number of bees gather around the completed cell, one of them initiates the food deposition phase. Immediately thereafter the number of interactions of the attending workers with the cell increases drastically. Some workers do not show up any more after their food deposition, others who remain perform the food deposition display several times, although we may not expect them to contribute much after their first discharge. Their agitated behaviour and the frequent cell inspections are

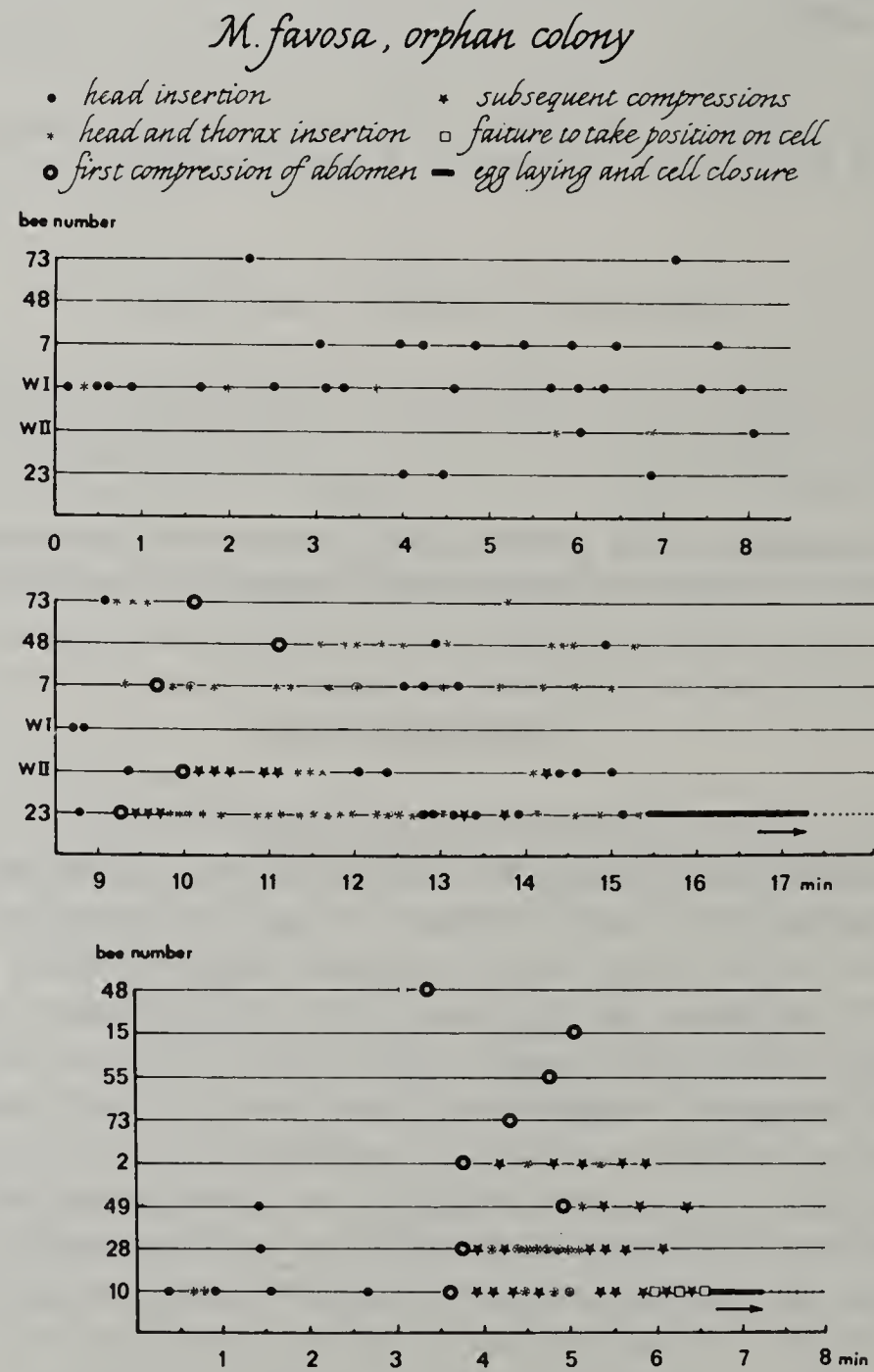


Fig. 7. – Interaction of worker bees with the cell during cell provisioning in an orphan colony of *Melipona favosa*.

³The kind and unselfish help of Mr. K. van Deursen, Paramaribo, to provide us with these colonies is acknowledged.

accompanied by pushing aside other interested bees. Generally, the bee with the most interactions with the cell is the one who lays the egg. The high degree of competition for this final possession of the cell is even reflected by the agitated pushing by other bees when the egg layer finishes the process by closing the cell.

Apparently, in *Melipona* the dominance in behaviour, obtained by overt aggression and in case of the queen in the form of ritualized aggression, leads to reproductive advantage of the dominant individual.

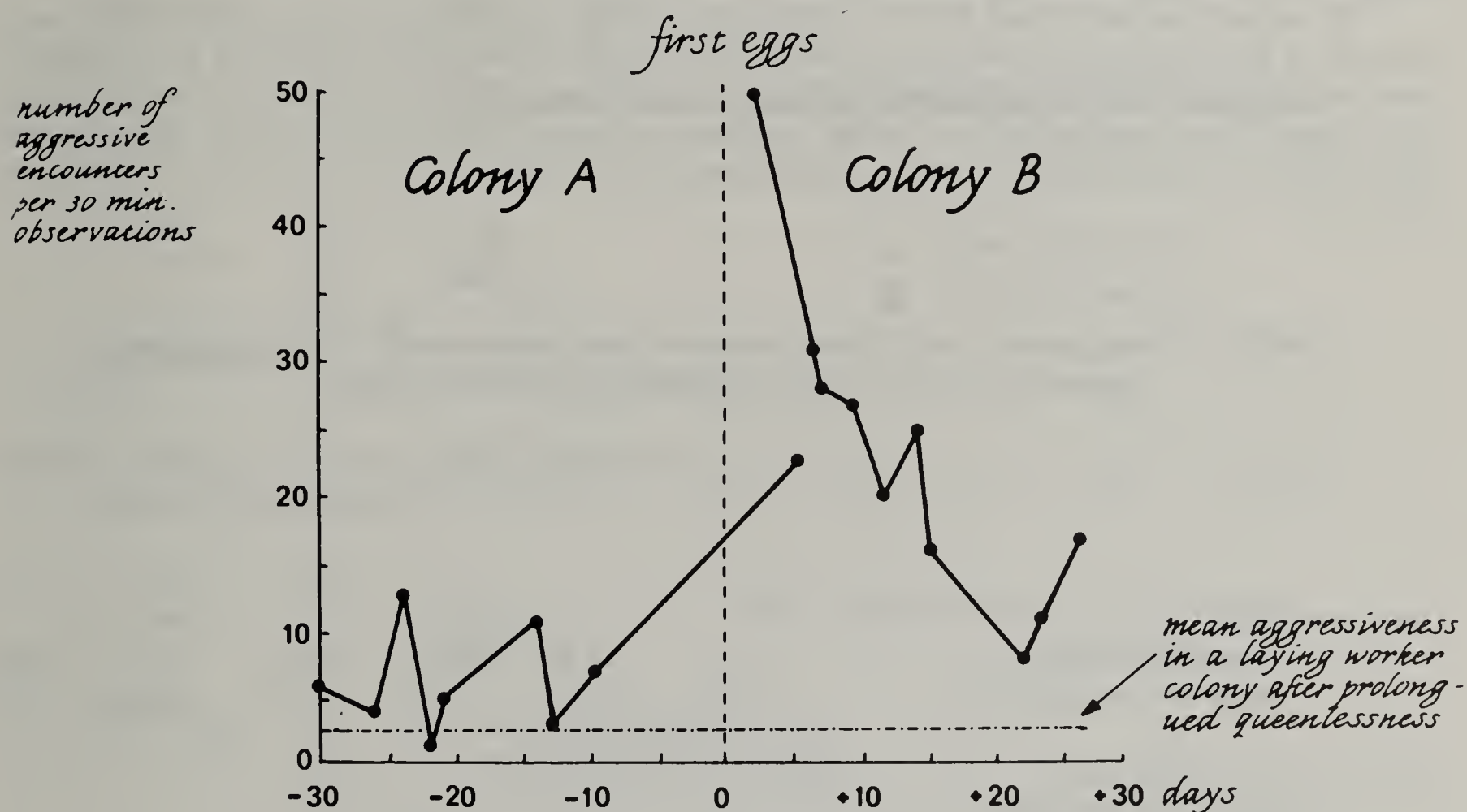
Functional Groups in *Apis mellifera* Laying Worker Colonies

The Aggressive and the Laying Worker

In contrast to this is the situation in laying worker colonies of *Apis mellifera*. The tendency to form a retinue around a laying worker is very low. Eggs are laid in very irregular patterns, several together in a cell. Like in bumblebees (Free 1955), egg laying by workers is accompanied by the occurrence of increased aggressiveness in the colony (Fig. 8). However, in distinction to bumblebees, aggressiveness and tendency to lay eggs are not correlated on the level of the individual bee. Prospective laying workers insert their abdomen into the cell before they are able to lay eggs and this performance continues once they get the ability to reproduce. Sakagami (1968) noted the same for *A. cerana* workers and coined this behaviour 'empty oviposition.'

An analysis of the behavioural elements of laying and aggressive workers in *mellifera* is presented in Fig. 9. This shows that these are distinct groups, the laying workers being submissive toward the aggressive ones. Each category continues to behave in this characteristic manner for periods of up to two weeks. It seems as if transitions from laying workers into aggressive ones or transitions in the opposite direction are very rare.

The aggressive bees are especially aggressive toward the laying ones, and, apparently, the latter are distinct from a third category, consisting of the majority of the bees, which we may call here the indifferent ones.



AGGRESSIVENESS IN LAYING WORKER COLONIES (*Apis m. mellifera*)
IN RELATION TO THE APPEARANCE OF THE FIRST EGG.

Fig. 8. — The occurrence of aggression per 30 min. observation periods in orphan colonies of *A. m. mellifera* in relation to the day on which the first eggs appear.

The behaviour of individual bees in laying worker colonies (*Apis m mellifera*)

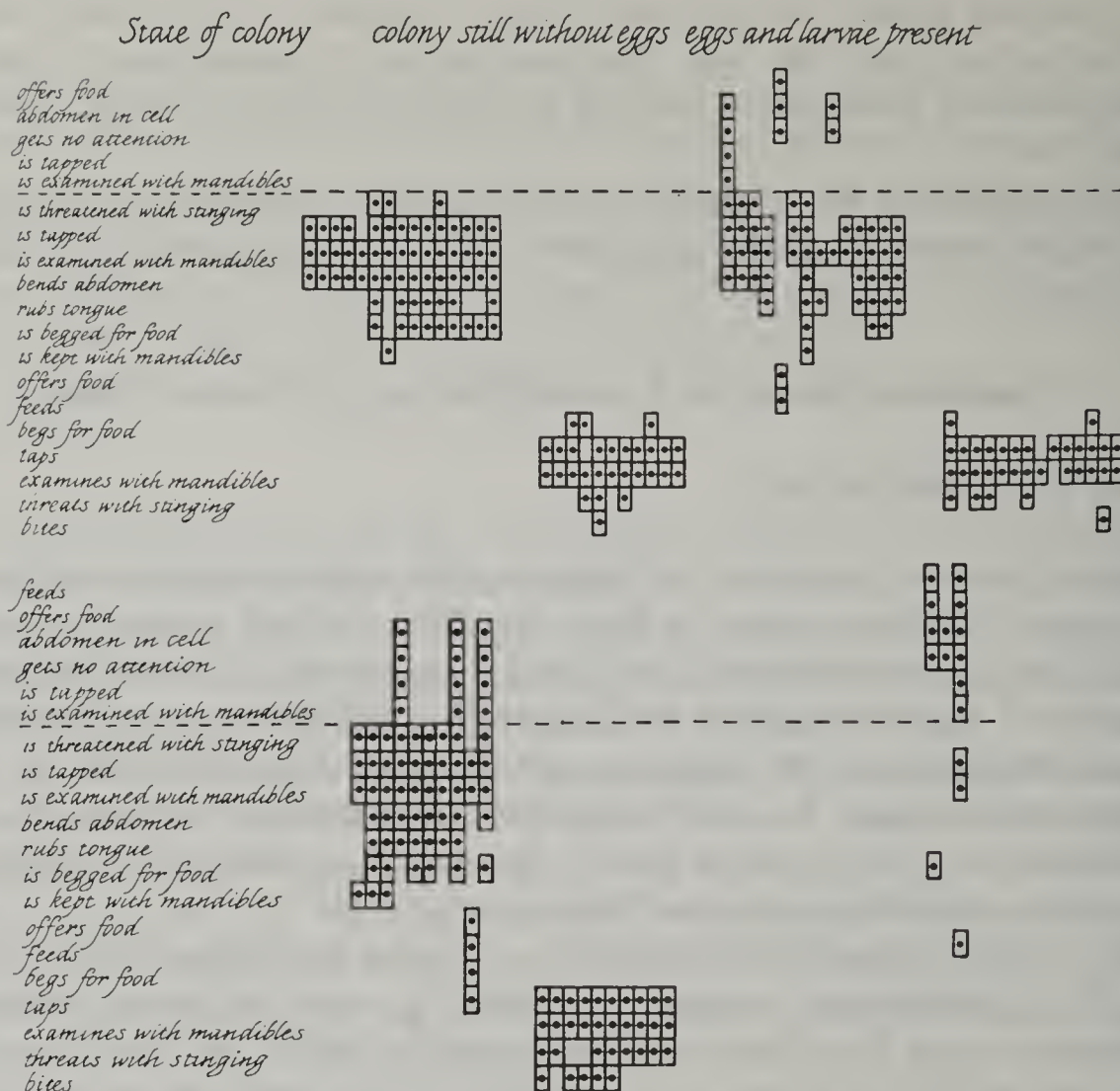


Fig. 9. — The occurrence of various active and passive behavioural characteristics in individuals involved in aggressive encounters in a orphan colony of *A. m. mellifera*. The several stages in the development into a laying worker colony are given separately. Above the dotted line the workers that were seen with their abdomen in the cell (in part “empty ovipositioning”) during the same observation.

In such colonies apparently the animals that are dominant in the reproductive sense are not identical with the behaviourally dominant ones.

In cooperation with Prof. Dr. W. Engels from Tübingen, Germany, the two groups of bees were studied on the correlation between their behaviour, the titer of the vitellogenin (the protein that is transported by the haemolymph towards the ovary, see Engels 1974) and the state of the ovary. The two types of bees were marked on the day they were recognized by their performance and up to one week thereafter were dissected to take a haemolymph probe and to study the ovaries. Table 2 gives the result.

Table 2.—Ovarial activity and vitellogenin titer in the haemolymph of egg laying and aggressive workers (*Apis m. mellifera*) in relation to aging.

		number of days after being recognized to belong to one of the behavioural groups					
		0	1	2	3	5	7
vitellogenin titer							
	laying worker bees	51.6	48.9	46.0	46.0	43.7	41.5
	aggressive worker bees	40.1	43.6	37.2	41.4	37.7	36.2
ovary activity of same bees							
	laying worker bees:						
	number of ovaries highly active	18	12	10	16	30	14
	intermediate active	6	4	4	6	5	6
	aggressive worker bees:						
	number of ovaries highly active	14	7	7	5	9	4
	intermediate active	18	15	13	17	21	16

While the egg laying bees have the highest percentage of vitellogenin on their first day, a value that decreases with increasing time, the aggressive ones have a lower percentage and more irregular time relation. Differences between the two groups are significant for the first days as is the difference between first and last day of the egg layers.

At the same time we see that the egg layers as a group have a high degree of activation of the ovaries; 100 ovaries contained eggs in the sausage stage while in 31 the maximum development was found in the still rounded oocyte. The aggressive ones are characterized by a lower degree of activity of their ovaries, 46 ovaries having sausage shaped eggs and 100 ovaries only rounded oocytes. Interestingly, both groups did not contain a single worker with resting ovaries. In laying worker colonies always a number of workers are present with completely inactive ovaries. These, apparently, are to be expected in the group of indifferent ones.

The Production of the False Queen

Recently we obtained through Prof. Dr. F. Ruttner, Oberursel, Germany, a very interesting animal: the worker of the honey bee race *Apis mellifera capensis*. This bee is very peculiar in having much more ovarioles than the workers of the other *mellifera* races, namely between 10 and 30. Furthermore, it has a well developed spermatheca. Most interesting of all is its capability to reproduce telytokously, that is producing female offspring without being fecundated. The animal has been described by Onions (1912, 1914), Jack (1916), Lundie (1954) and Anderson (1963). In cooperation with Prof. Ruttner we studied the events after introducing these bees in queenless observation hives of *A. mellifera mellifera*. Figure 10 gives an example of what happens. Ten freshly emerged and marked *mellifera capensis* bees were introduced in a shortly before dequeened colony of *mellifera mellifera*. Soon one of them became a false queen, while the others were eliminated by the colony. In other cases a few false queens remained, each having a retinue. They do not show any antagonism against each other when they meet.

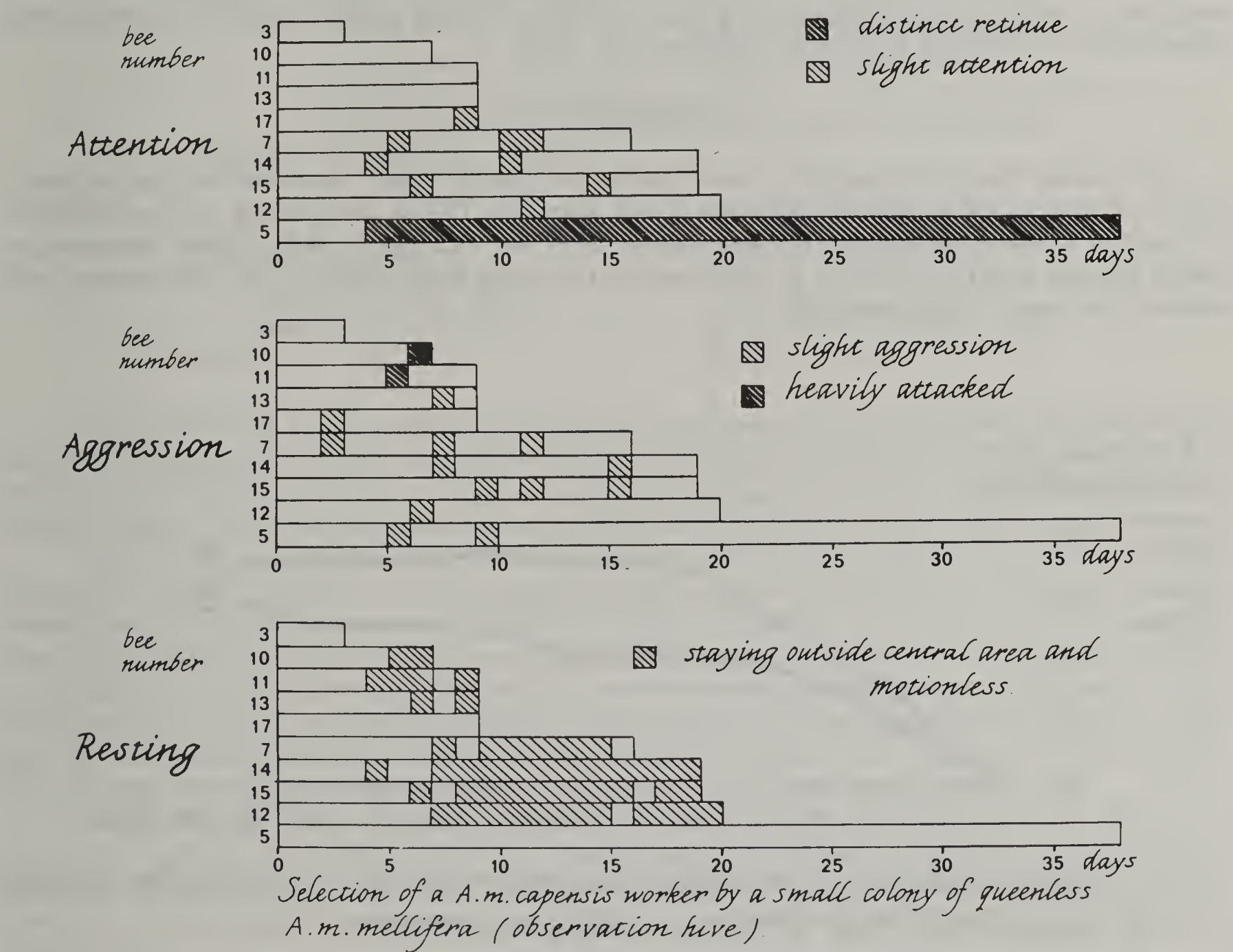


Fig. 10. – Some of the behavioural interactions during the selection of one *A. m. capensis* false queen out of 10 workers of this race introduced in an orphan colony of *A. m. mellifera*.

Egg laying by the false queen may start after about a week and she may produce up to about 200 eggs per day. However, mortality is high. When after about three weeks the first *capensis* workers emerge, the *mellifera* workers attack them. They are balled as is known from *mellifera* workers that meet a disturbed queen (Yadava and Smith 1971a, b, c), and are thrown out of the colony. This may happen also with the false queen during the following weeks of tremendous aggressiveness. Finally, only old *mellifera* and probably a few *capensis* workers survive. The false queen behaves as if she is the queen, laying eggs singly in a cell, in the centre of the bottom.

In a colony of only *capensis*, however, the behaviour of the many laying workers is comparable with *mellifera*: many eggs irregularly placed in the cell, and with submissive behaviour of the laying workers and a separate category of aggressive bees.

We did a few experiments concerning the dominating behaviour of the *capensis* false queen. When 50 *mellifera* worker bees upon emergence are placed together in a cage, a number of them will develop active ovaries and will produce eggs (Velthuis 1970a). With a dead *mellifera* queen amid them, this activation is inhibited by the pheromones still present on the queen's body (Verheijen-Voogd 1959). Such queenright groups of worker bees eagerly draw comb from a piece of foundation.

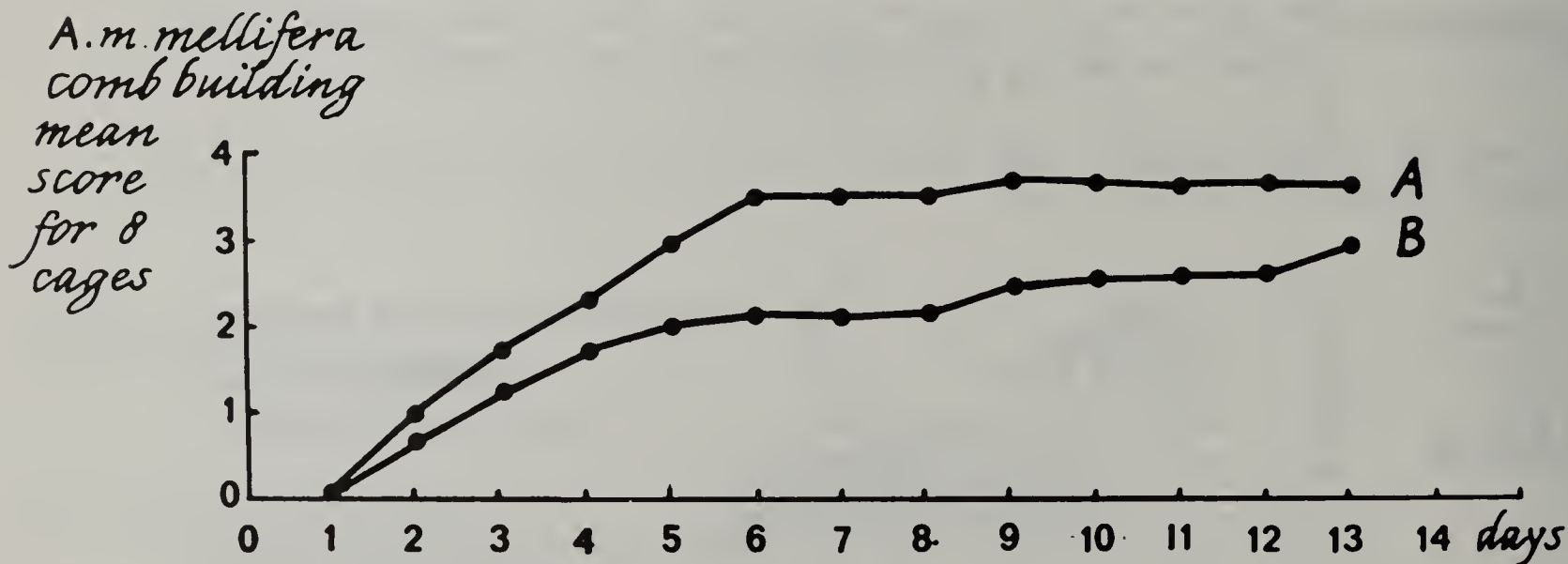
When 50 *capensis* workers were placed together, they did not develop active ovaries nor did they draw comb. A dead *mellifera* queen, evoking retinue behaviour in *mellifera* workers, was not noticed by them.

When 12 *capensis* workers were each placed among 50 *mellifera* workers, all proved to be able to inhibit ovarian activity in these workers. When, after termination of this experiment, their mandibular glands were excised and offered to a second group of 50 *mellifera* workers, these glands had similar effects as the mandibular glands of virgin *mellifera* queens, so that the glands probably produce queen substances. Their effects on comb construction in both experiments are given in Figs. 11 and 12. Table 3 gives the egg production observed in the second experiment.

The same was studied from the chemical point by Ruttner, Koeniger and Veith (1976), who were able to isolate from the heads of laying *A. mellifera capensis* workers the 9-oxo-decenoic acid characteristic so far for all *Apis* queens (Shearer et al. 1970).

Concluding Remarks

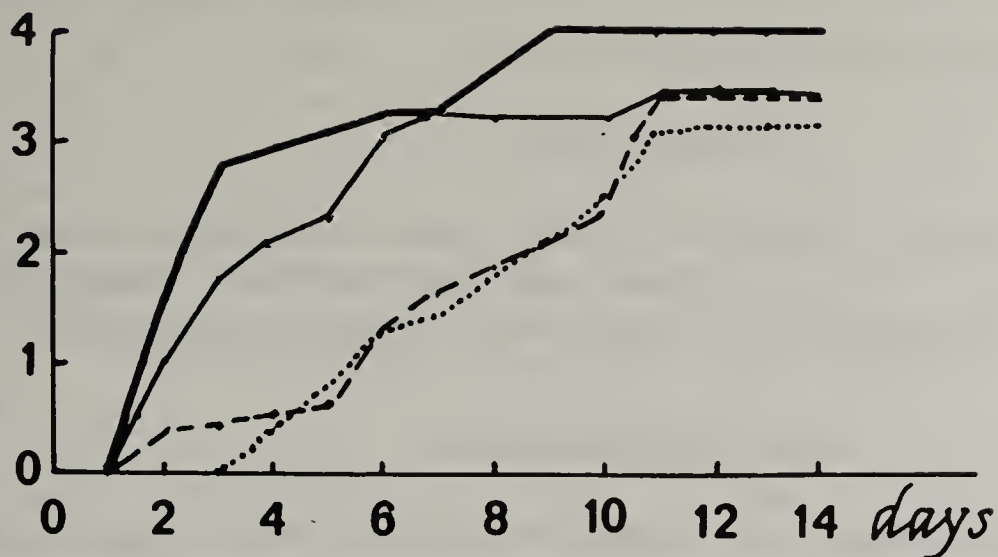
The prevention of egg laying by social bees other than the queen occurs at two distinct levels. One is the level of the hormonal regulation of the oogenesis. This is encountered in some Halictids, for instance *Evylaeus marginatus* (Plateaux-Quenú 1959, see Michener 1974 for further examples), in several stingless bees (Sakagami et al. 1973) and in the honey bees. These species have workers with undeveloped ovaries when queenright.



A : cages with one *A. m. capensis* worker and 50 *A. m. mellifera* workers
B : cages with only 50 *A. m. mellifera* workers

Fig. 11. — Comb building by *A. m. mellifera* workers in cages with or without one accompanying *A. m. capensis* worker.

A. m. mellifera
comb building
mean
score
for 8
cages



- mandibular glands of *A. m. mellifera* queens added.
- mandibular glands of laying *A. m. capensis* workers added.
- no mandibular glands added.
- mandibular glands of young *A. m. capensis* worker added.

Fig. 12. — Comb building by *A. m. mellifera* workers in cages provided with mandibular glands of either *A. m. mellifera* queens, laying *A. m. capensis* workers or young *A. m. capensis* workers.

Table 3.—Number of eggs present in the comb after 14 days of exposure of resp. (a) the mandibular glands of virgin *A. m. mellifera* queens; (b) the mandibular glands of laying *A. m. capensis* workers; (c) the mandibular glands of young *A. m. capensis* workers; and (d) control extracted dead worker bee bodies without glands to 50 *A. m. mellifera* worker bees.

	cage numbers	1	2	3	4	5	6	7	8	mean
<i>A. m. mellifera</i> queen		0	0	0	0	0	0	0	0	0
capensis laying worker		0	0	0	0	0	0	0	0	0
capensis young worker		48	24	24	40	38	37	22	43	34.5
controls		28	11	0	6	15	29	47	2	17

The other level is a behavioural one. Here use is made of overt aggression or ritualisations derived from aggression. This is exemplified by other Halictids, for instance *Lasioglossum zephyrum* (Brothers and Michener 1974), to some extent the bumblebees (Free 1955, but see Röseler, 1974) and the majority of the stingless bees. These workers may sometimes lay eggs when queenright.

The evolution of specific queen pheromones might well coincide with the development of larger populations inside the nest. In those cases the single queen needs to develop a warning system to extend her influence beyond the reach of her mandibles and sting. Such a signal could well be derived from her sex pheromones, a factor in a communication system that bears directly upon reproduction.

The presence of such specific queen pheromones seems to be independent of the level at which the reproduction by the workers is controlled. The fact that the queen honey bee produces the major part of her queen pheromone complex in her mandibular glands also points in a communicative direction, since this gland in many bees is related to several kinds of communication.

With increasing polymorphism the potencies of the two female castes become more distinct. In fact, in the orphan colony the workers are brought back in an antique situation in the evolution of their species: the females are all more or less alike. What they do in this situation depends on what remains of their antique equipment, thus pointing to the origin from which both queen and worker are derived.

For *Apis* the capacity of the worker to develop into a false queen is limited, although there may be differences between species. Within the race *A. mellifera capensis* this situation does not differ

much from that of *A. m. mellifera*. However, transfer of a *capensis* worker into a queenless *mellifera* colony shows that the *capensis* is more able to produce specific queen substances than the *mellifera* worker. It is becoming increasingly interesting to know how worker bees recognize intermediate females and how this relates to the intriguing situation, that the laying worker at the same time is dominant in a reproductive sense and behaviourally submissive.

Acknowledgment

Of the many students who contributed to the unpublished research mentioned in this paper I may mention especially Mrs. F. Oomen-Kalsbeek and Mrs. M.A.J.J. Streenstra-Goumans. The assistance given by Miss H.A. van Esveld in these experiments is equally appreciated.

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Recent Advances in the Orientation and Learning of Honeybees

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Problems in orientation of honeybees were mainly concerned in the last 30 years with foodgathering, flower constancy and mutual communication by dances (see comprehensive review by K. v. Frisch 1967). The suncompass guides the foragerbee menotactically towards the goal. When the sun is hidden behind clouds the pattern of polarized light on the blue sky indicates the position of the sun. R. Wehner (1976) will report on recent research and problems in this field.

When the bee approaches the goal, she is attracted by the odour, colour and pattern of the blossoms and she uses these cues for a successful reorientation. Studying this reorientation in more detail we came across new problems of learning, relearning and forgetting, which I hope will promote our understanding of the physiology of the learning process in principal. After his return to the hive, the gravity sense in combination with the suncompass give the basic parameter, when the dancing bee has to transpose the angle between sun and feeding place into the gravity field.

1. Orientation in the Geomagnetic Field

In this connection we have been faced for a few years with quite a new problem in orientation: the indication that the direction to the goal by the wagging line of the dance is influenced by the geomagnetic field; following a diurnal course we register a small deviation ("Missweisung"), which is correlated (1) with the dynamic change of the total intensity of the geomagnetic field during the day; and (2) with the angle between the wagging line and the angle of the inclination (Fig. 1). The "Missweisung" (Mi) then follows this function:

$$Mi = eH_2 \pm \frac{r}{2} \cdot (eH_2 - eH_1) \cdot \ell$$

eH = statistic effective field power = $\log (\Delta F + 1) \cdot \mu \cdot \sin a_m$

μ = factor of permeability

ℓ = scale factor = 0,2

ΔF = Variation of total intensity of the geomagnetic field in a given time

a = angle of the dance related to gravity

a_m = angle of dance in relation to inclination

r = Reygleigh constant (= 0,4)

In the compensated geomagnetic field the dances show no deviation (Lindauer and Martin 1968, 1972, Martin and Lindauer 1973). The Earth's magnetic field however is not disturbing the orientation. In recent times more and more records are published stating that animals orient themselves in the geomagnetic field correctly; the experiments of Wiltschko (1973) and Keeton (1969, 1971) on birds, of Becker (1971) on termites may be mentioned as the most convincing ones. However, the sensory basis of this orientation mechanism is still unknown. Akoev, Ilyinsky and Zadan recently (1976) found that the electroreceptors of electric fishes react to magnetic fields in the range of $\frac{1}{2}$ Gauss (this is approximately the intensity of the earth's magnetic field). We suppose that in bees no special "magnetoreceptors" exist; induction or paramagnetic effects may be involved in the perception mechanism.

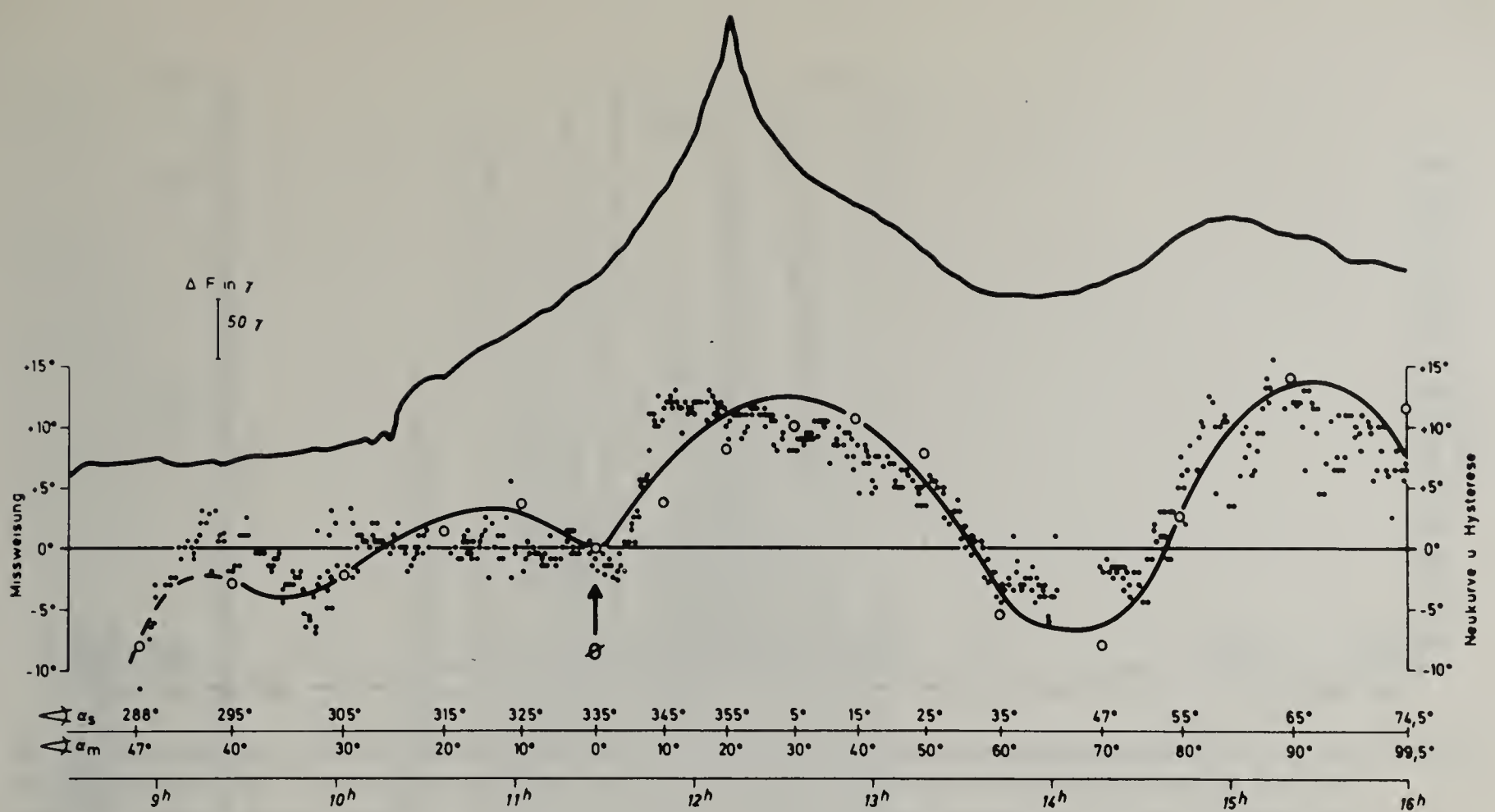


Fig. 1. – The feeding table was located 400 m southwards of the hive. During the day (8.30-16.00) the magnetic variation was measured (curve above: ΔF in γ). Simultaneously the “Missweisung” of the dances in the hive was recorded; each spot represents 10 wagging lines of one dance. The curve below is the function described in the text; it fits well into the real data of the “Miß-weissung”.

Some surprising results we got from our recent experiments: bees use the diurnal periodicity of the geo-magnetic-field as a timer.

The vectordiagram in Fig. 2 clearly shows a periodic change in the intensity of the horizontal and vertical component, and a dynamic change in direction of the inclination and declination. This 24-hour periodicity which we have registered in Würzburg since Sept. 1973, is disturbed only by magnetic storms. We have tested time-trained bees in an artificial aperiodic magnetic field. As Fig. 3 demonstrates, the bees no longer remember the exact feeding time.

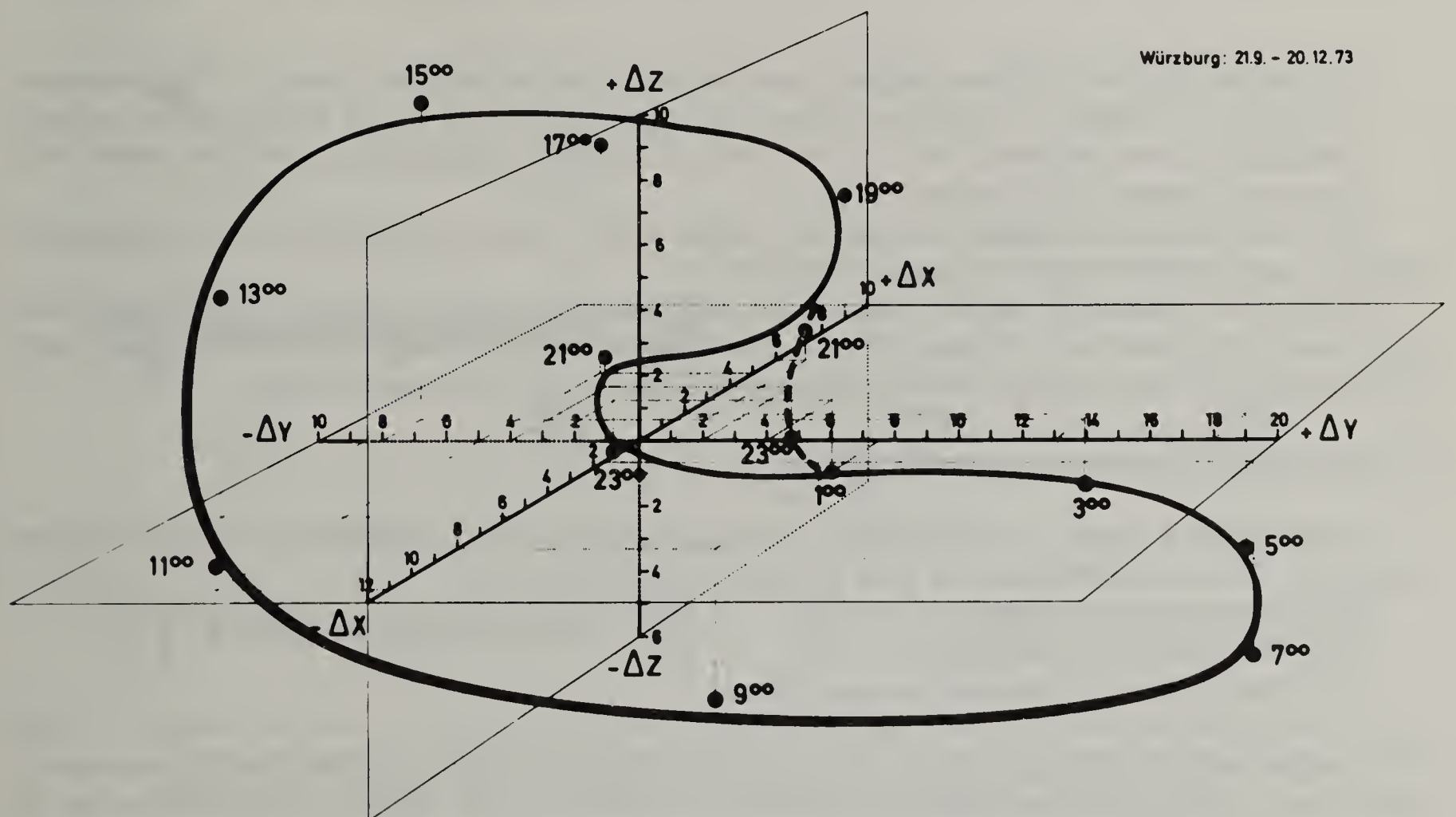


Fig. 2. – The dynamic variations of intensity and direction of the geomagnetic forces follow a 3-dimensional vector diagram. This vector-diagram is characteristic for each geographic latitude. Δx and Δy = horizontal components, Δz = vertical component.

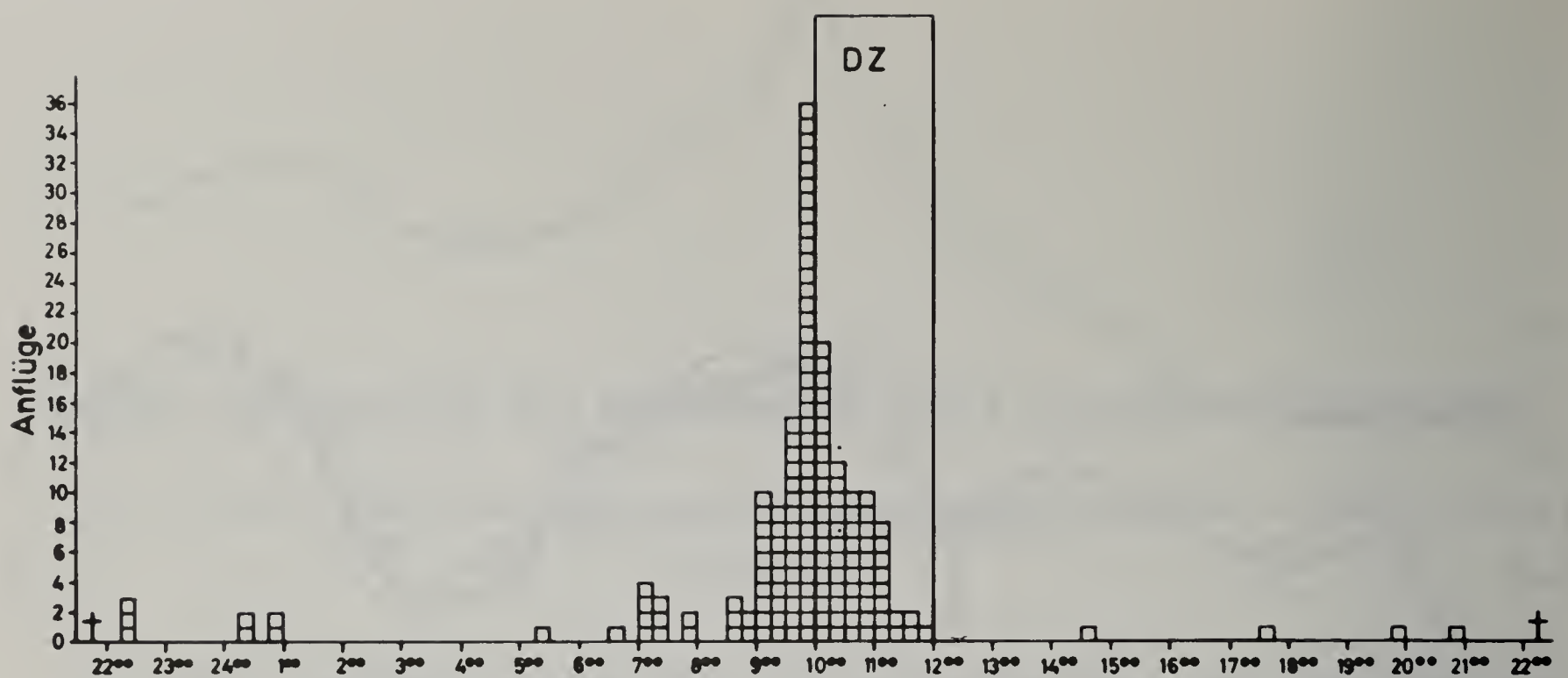
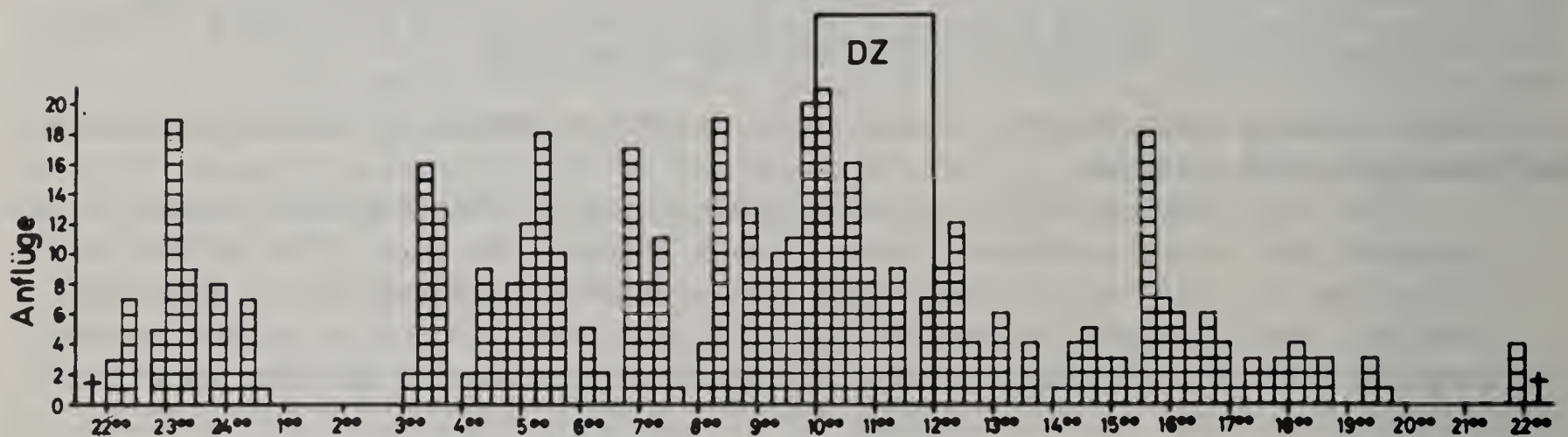


Fig. 3. — In an artificial illuminated room bees were trained for a feeding time 10-12.00^L (constant light, LL). In the test the bees remembered well this time (Figure above): each square represents a spontaneous visit on the feeding table. If the normal magnetic field is disturbed by a 10 x stronger, aperiodic field the time sense of the bees is disturbed (Fig. below).



Furthermore, from 19 time-training experiments in the last summer, under normal magnetic conditions, 4 failed; i.e.; the bees arrived too early or too late at the feeding table, or their approaches were scattered over a few hours. Exactly on those days our Gauss-meter had registered magnetic disturbances.

We also recorded disorientation in time when a bee colony was translocated in geographic latitude, i.e., from Würzburg to the polar circle (Fig. 4).

Only after 7 days had the bees resynchronized their inner clock in relation to local conditions. There was no light-dark shift in these experiments; however the periodicity of magnetic intensity and of the direction of the magnetic fieldlines differed strongly in these different latitudes.

2. Orientation of Bees as a Learning Process

Orientation is always connected with some learning processes. In the following I will discuss only three of the questions which we have investigated in the last years.

- (1) Time-coupled learning.
- (2) Race specificity in learning.
- (3) The problem of relearning and extinction.

Time-coupled Learning. — *Economy* in learning is a prerequisite for any successful orientation. That means: different learning tasks are confined to restricted phases in their foraging flight. Fig. 5 will explain the problem: a naive bee arrives at a feeding table, where she finds sugar solution placed on a blue card; in the moment she alights on the table and extrudes her proboscis the blue card is carefully removed and a yellow one appears. When she takes off — regularly she flies around the goal

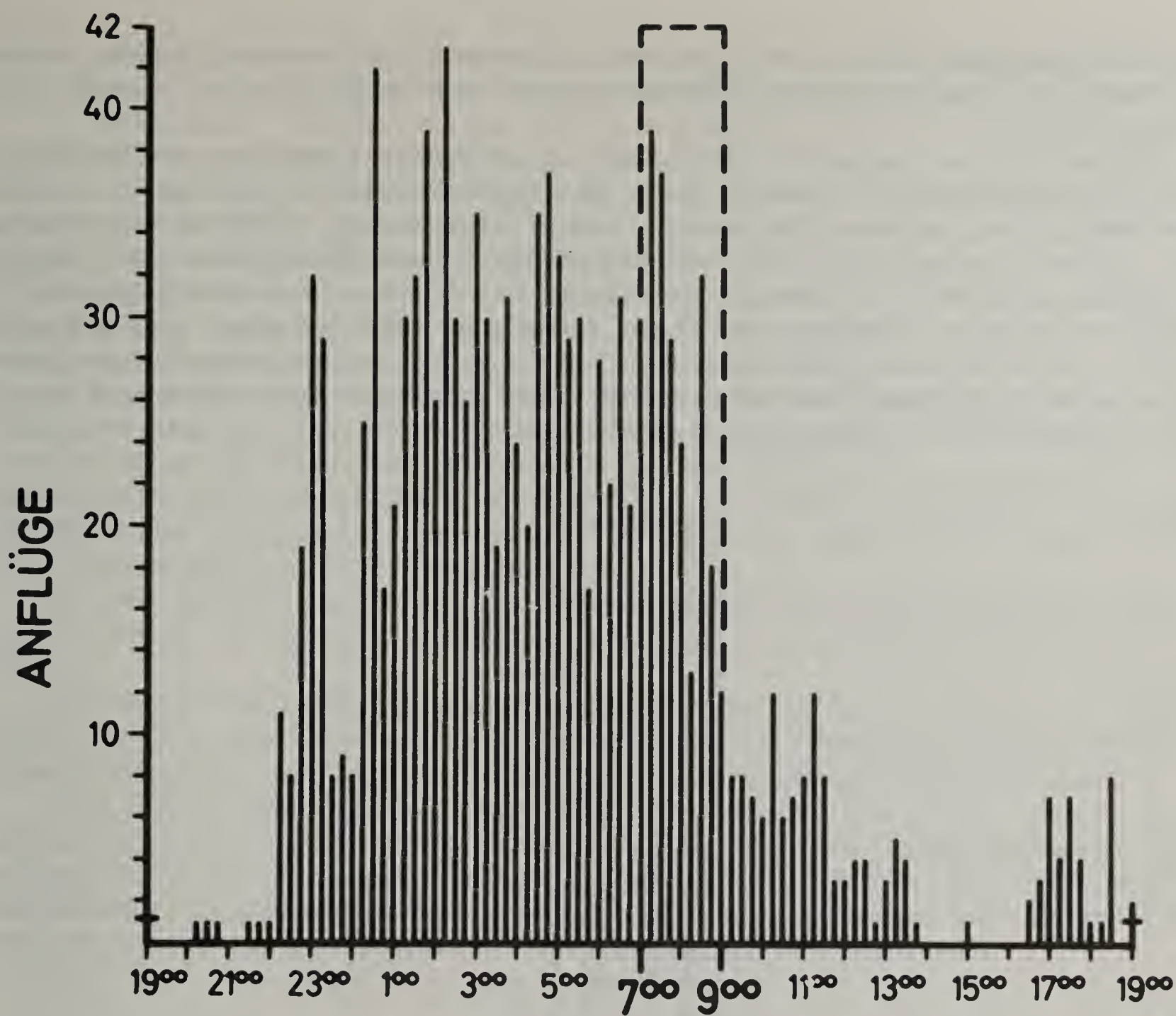


Fig. 4. — In Würzburg a group of bees was trained for a feeding time 7-9.00; displaced to Messaure at the polar circle there were disoriented in time.

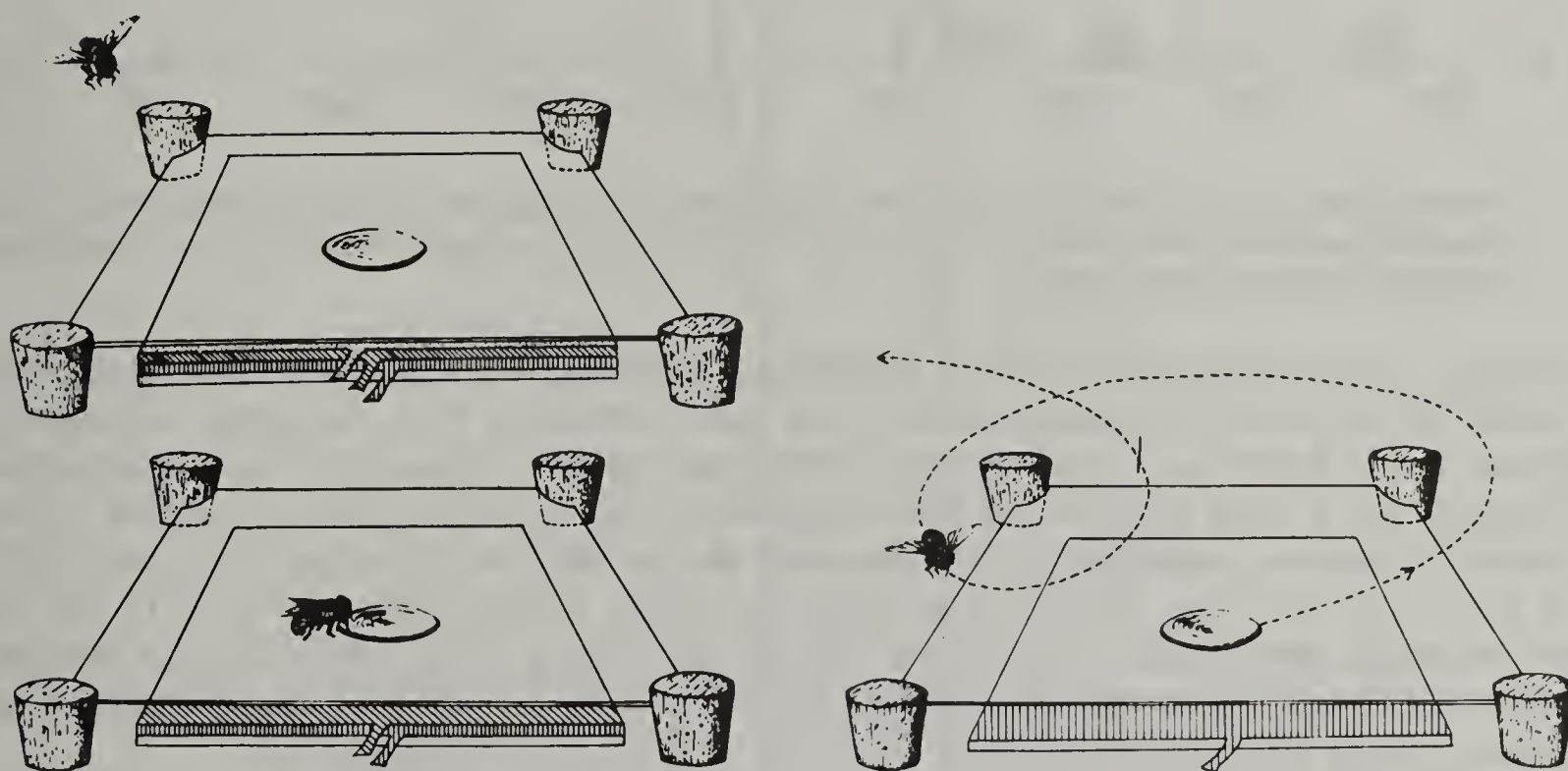


Fig. 5. — Approaching the food source the forager bee sees a blue card beneath the sugar solution. While sucking a yellow card appears; in flying off a green card is presented. When the bee returns blue, yellow and green are presented one beside the other. The bee chooses blue as food signal.

for a few seconds — a green card is visible. We know for sure that this forager bee will return to the table after delivering the nectar in the hive and will search for the coloured cards as food signal. However what colour did she associate with food? To find this out, we offer to the returning bee a

blue, yellow and green card, one beside the other. Unanimously the bees choose the blue card and demonstrate that only the *approach flight* is important to learn the colour of a nectar flower (Opfinger 1931).

Menzel (1967) has analyzed this phenomenon in more details; he found that only 3 seconds are reserved for this learning task: 2 seconds before the bee tips her tongue into the sugar solution and 1 second while sucking. By this, all the remaining time of a foraging trip — which can take 30 min. or more — is free for coding other cues for orientation. This is a remarkably economic way of learning!

Koltermann (1969, 1971) has gone a step further: he fed the bees from morning to evening at a neutral, i.e., “unscented” feeding site; at 10 a.m., however, he added to the sugar solution Geraniol scent for some minutes. Bees learn a scent signal very fast — 99% positive choices against a control scent after one learning step. The author wanted to find out whether and in which time bees will forget this signal when he continues feeding without scent.

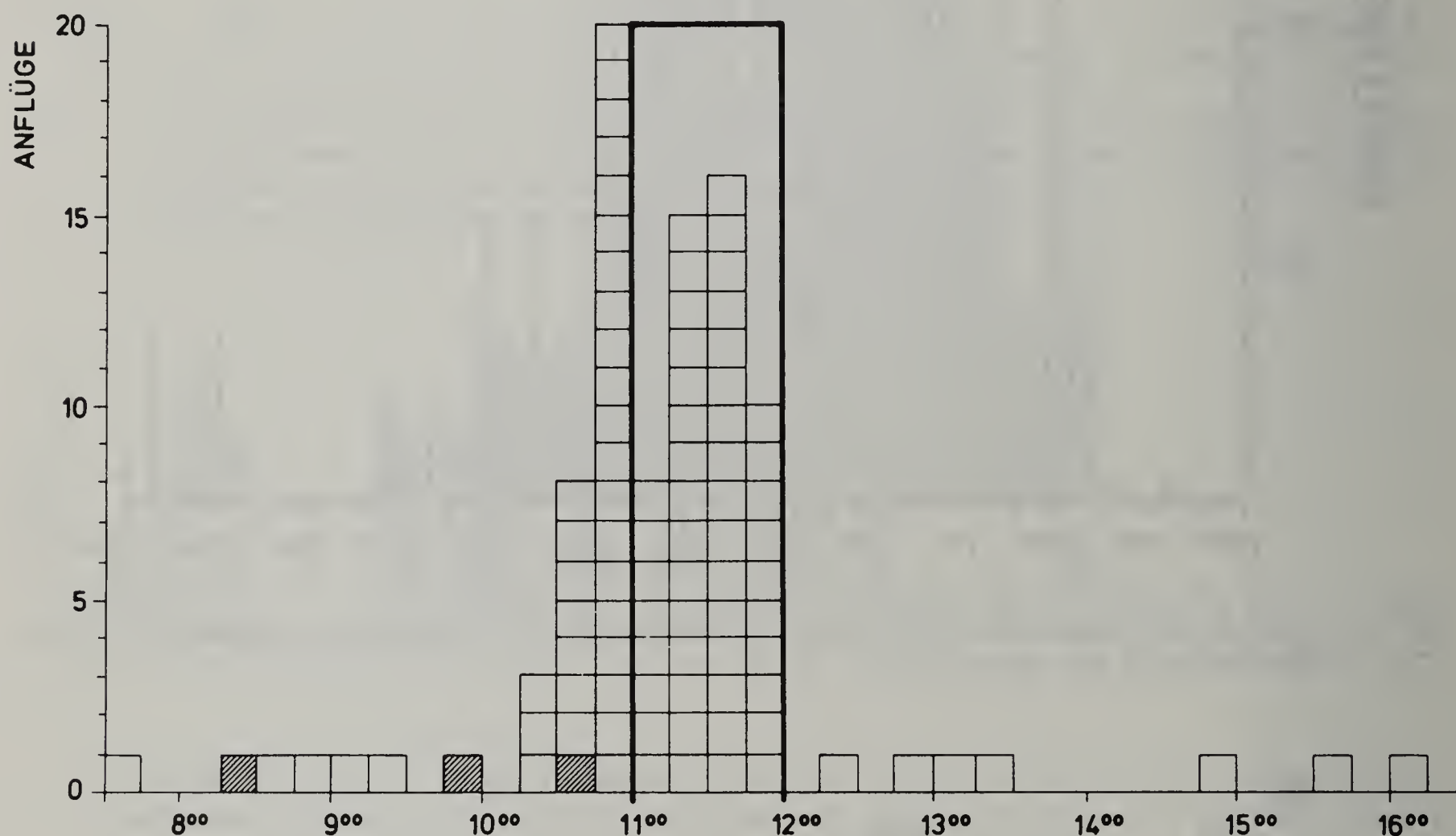


Fig. 6. — Feeding time (11-12^h) and blue colour were combined as learning unit. During training these two signals remained constant. In the test the bees choose correctly the time signal and the colour. (Striped squares: negative choices for grey cards).

Indeed, in the course of the day a continuous decrease of positive decisions for the trained scent could be observed. The next morning the bees seemed to have forgotten completely the conditioned scent. At 10 a.m., however, the training time of the previous day, the bees remembered that Geraniol was a food signal, what was demonstrated by a sudden peak of positive decisions. Furthermore, in another training series, the bees were able to associate the odour of Geraniol with the feeding time at 10 a.m. and the odour of Thyme with the feeding time at 3 p.m. In the end, 9 different points of time within 1 day linked with an odour signal could be entrained. A masterpiece of our bees — not only concerning the learning capacity but also of their time sense! The same results were obtained when different colours were combined with different feeding hours.

As a general rule we can state: Forager bees are not conditioning single components as learning signals; they combine the values of different cues presented together. This statement is confirmed by recent experiments of my student Bogdany (1975 in preparation): he has dissociated “compound learning” by changing one of two components in a discontinuous nonlogical way.

1. Experiment. — Bees are fed every day from 10-11^h on a blue card, “Blue” being food signal. The control test confirms that time and colour were conditioned as learning set. In the next series the training time remains constant while the colour signal is changed from one day to the next:

blue on the first, green on the second and so on. Contrary to the control experiment where time and colour remained unaltered (Fig. 7), bees did not learn either training colour nor training time.

2. Experiment. — We train the bees for the food signal “Blue”, but the training time over a period of days is not constant, we change it from 8-9 a.m., to 4-5 p.m., to 11-12 a.m., to 2-3 p.m., to 10-11 a.m., respectively. In the test the bees are not only confused with time, as expected, but also with colour signal (Fig. 8). The learning set: colour + daytime offered no logical combination; during training therefore the isolated components could not be associated separately in the memory.

3. Experiment. — A combination of *training time* and *odour* gives the same result (Fig. 9). Note, that only before and after training time negative choices are recorded. When scent and time-signal are decoupled again orientation to both signals is disturbed.

4. Experiment. — If we add a third signal from another modality, i.e., if we combine *trainingtime*, *odour* and *colour*, then a still more solid memory unit is created. We dissociate from this 3-unit-learning-set one component. The result is that the remaining two components still will be combined in the reading out process. If we dissociate 2 components, only that period which coincides logically with the conditioned combination (training time 3-4 p.a. yellow) records no negative choices for the constant signal, i.e., for the odour (Fig. 10).

As a side remark I may mention, that these findings meet increasing interest by psychologists; they may give us a better understanding of the learning process in principal. Another remark I want to add:

BOECKH (1976) (in this volume) reports on multimodal interneurons, which are individualistic in their activity. It would be of extreme interest, whether this multimodal individuality develops step by step in ontogenesis or whether it is the effect of personal experience by adaptive learning.

Race Specificity of Learning. — Orientation from hive to a food source demands that the scoutbee selects a few striking orientation cues from the environment as learning signals, so that she can return on the same way and can recognize the goal on the next trip. It is essential for location and identification of the goal that only those cues are selected and conditioned which are invariant and significant from one trip to the next, even if the environmental conditions change.

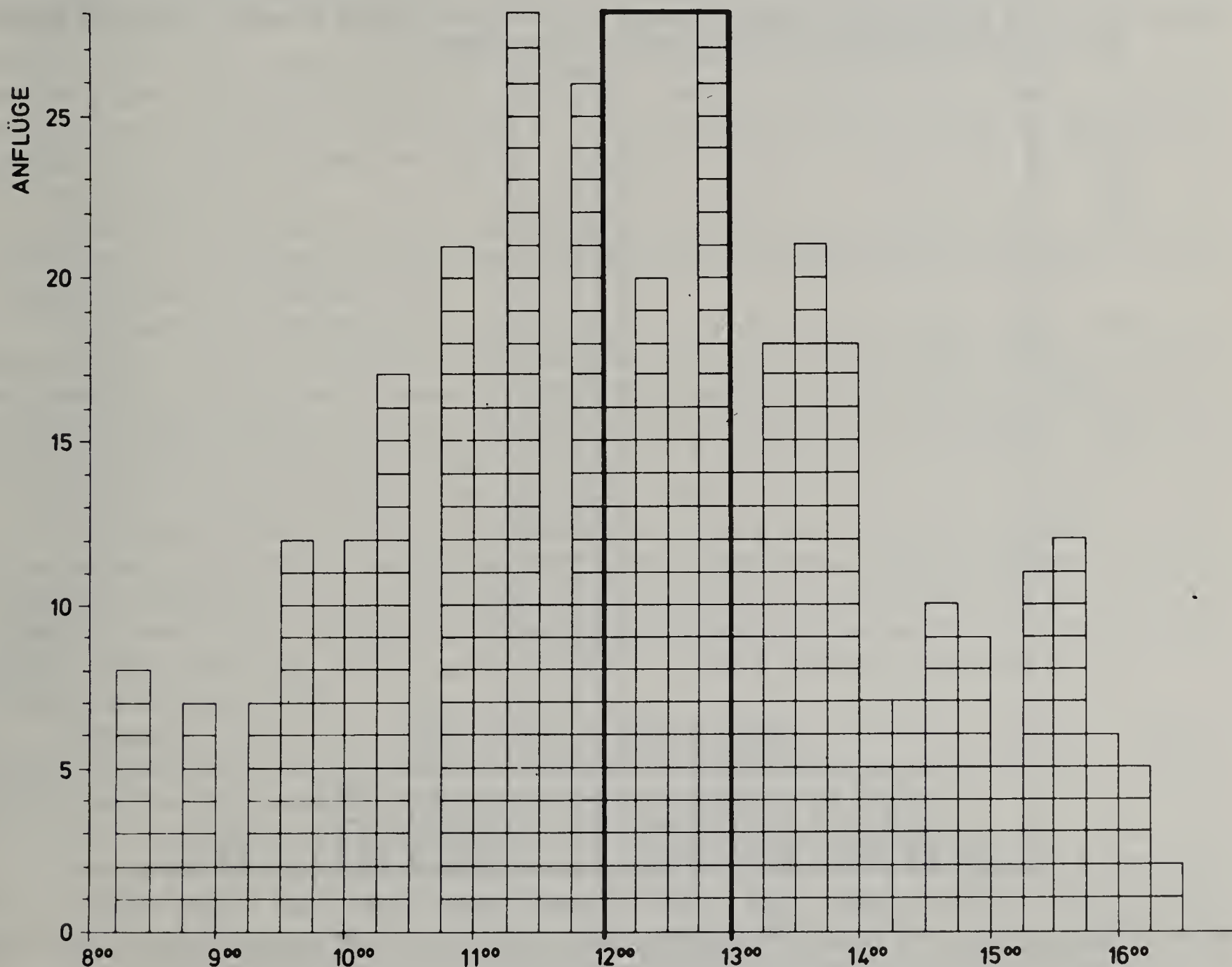


Fig. 7. — Colour signal in training changed, time signal was constant. The bees were disoriented also in time.

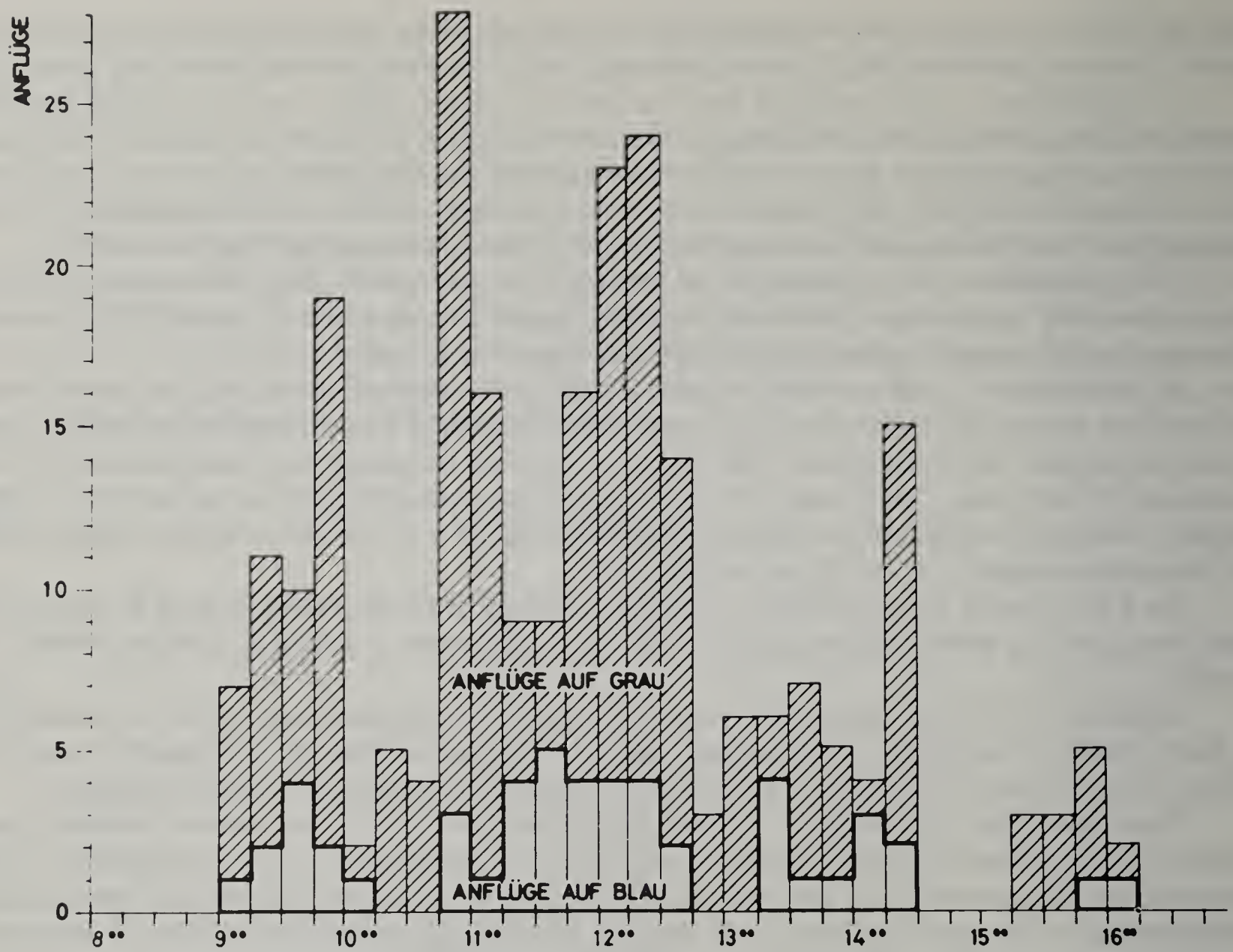


Fig. 8. – The colour signal remained constant, however the feeding time changed from day to day. In the test, the bee were disoriented not only in time but also in colour training.

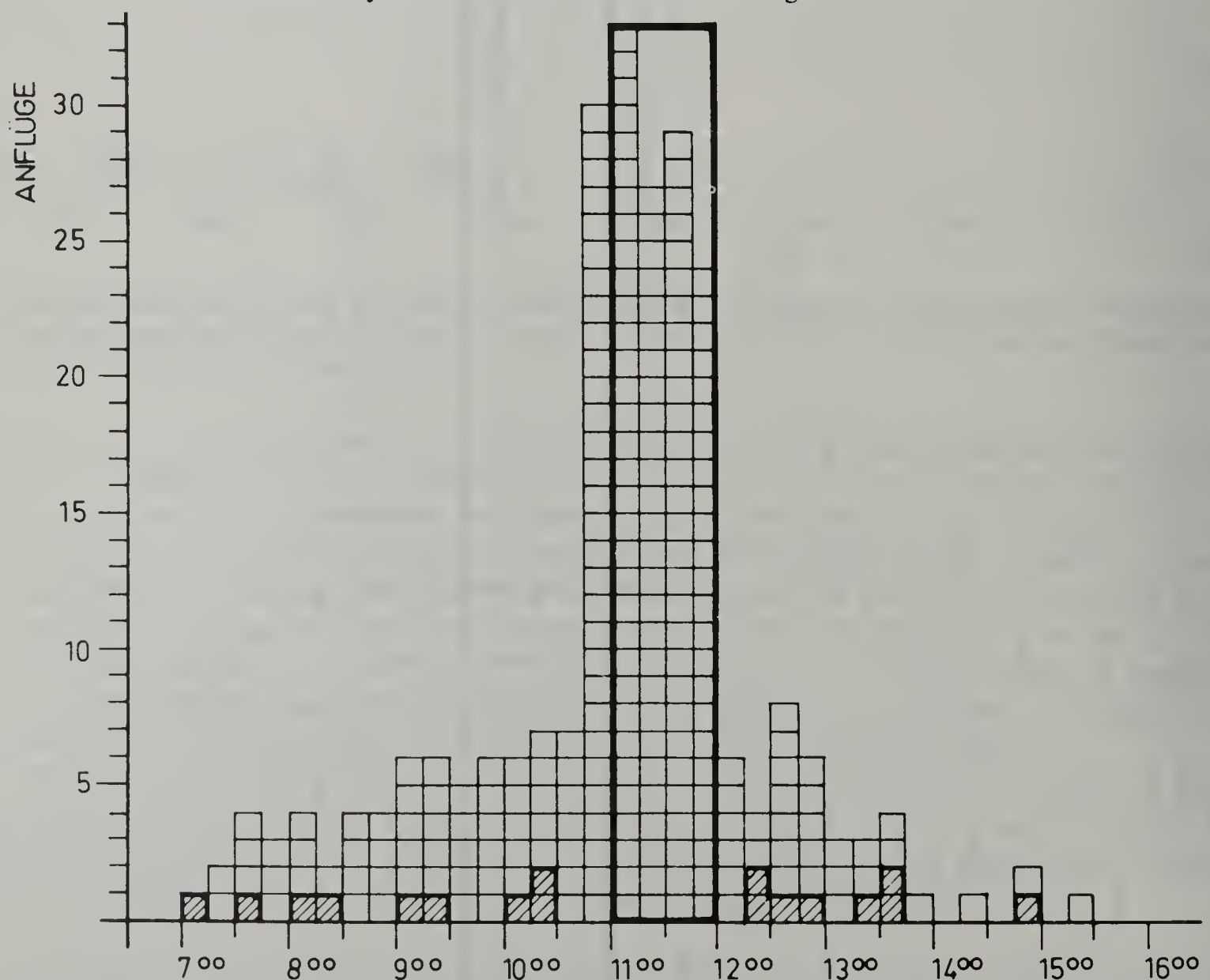


Fig. 9. – Time signal (11-12^h) and odour (Benzylazetat) were constant. Note, that negative choices for the control odour (Lavendel) were recorded only outside the training time.

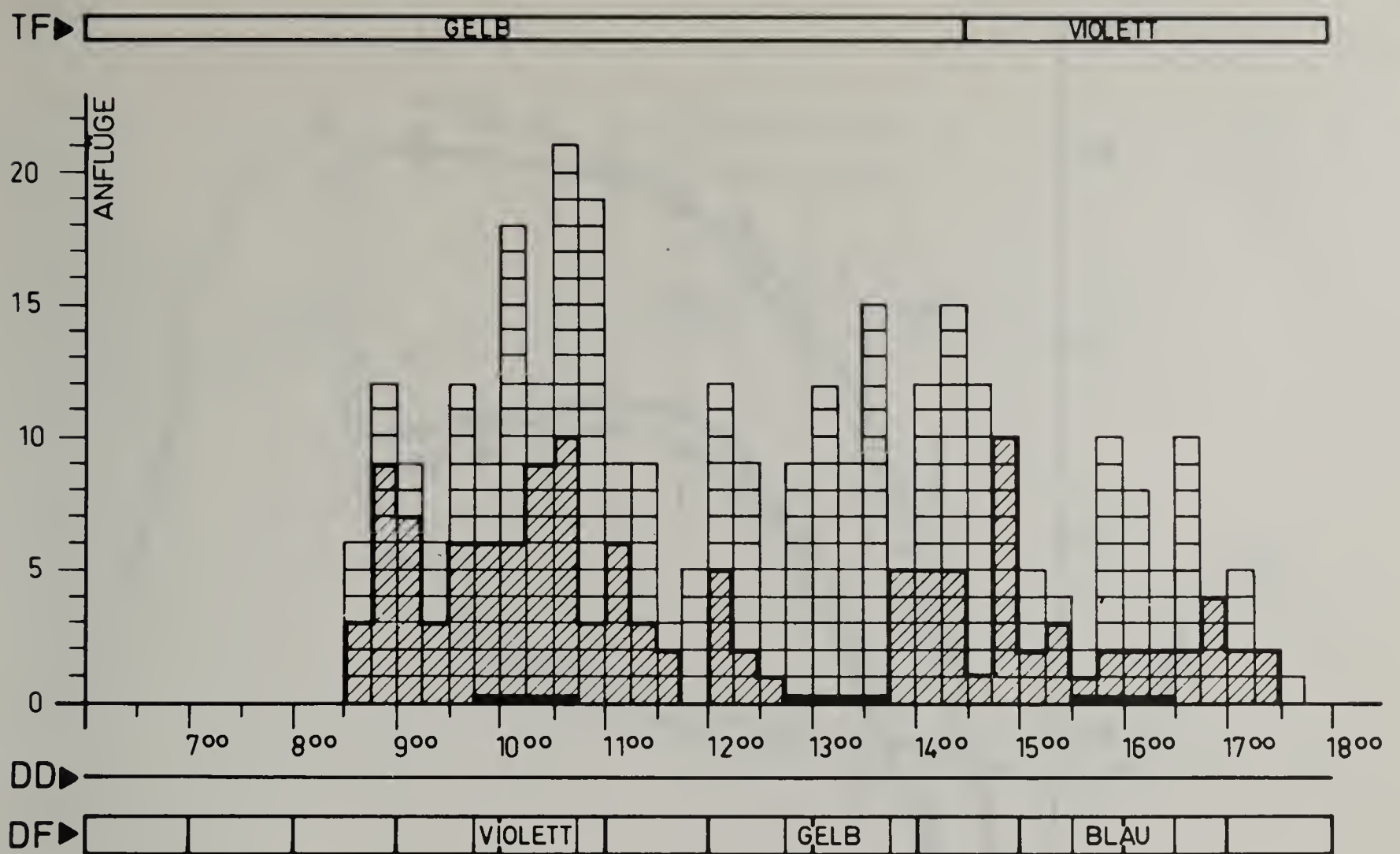


Fig. 10. – Learning signals hat to be encoded: 1. Odour (Rosmarin) which was constant, 2. colour (variable), 3. Time (variable 9.45-10.45, 12.45-13.45, 15.30-16.30h) When odour, colour and time corresponded with the training situation (12.45-13.45) the positive choices were optimal.

The work of my students Lauer (Lauer and Lindauer 1971) Hoefer (Hoefer and Lindauer 1975, 1976), Koltermann (1973), Menzel (1967), Kriston (1973) gives evidence of a *rankorder* of potential learning signals. When sugar solution is offered together with the signals scent, colour, and pattern, and we present these signals in the test separately, scents are learned best and fastest, colour is in second place, and pattern comes last. This rankorder exists also within one single modality: violet is learned better than blue, green and yellow; flowerlike odours like Geraniol better than the stinking fatty acids, as capron-acid.

In all these experiments we were surprised on the uniformity of the learning curves: between individuals and even between colonies there were practically no differences as long as we used bees of the same species and of the same race.

The results are quite different however, when we test another race. Fig. 11 gives evidence that this rankorder – we may call it learning disposition – is genetically fixed. The experimental setup is very simple: a black star in the center of a round table indicates where food is to be found. The bee has to learn that a black star at a fixed location means food. When the forager returns to this spot, we test whether the *star* itself (the pattern) or the *center* of the table (the location) is encoded as food source, the star being located now on the edge of the table.

The learning curves are strikingly different between two races. The italian-bees (*Apis mellifera ligustica*) prefer the *pattern*, the carnica-bees (*A. mell. carnica*) the *relative position* of the goal as signal for orientation. In many other orientation situations this race specificity in learning optical signals was confirmed – as long as additional landmarks could be put in relation to the goal. In an uniform environment the learning curves of both races were identical. (Lauer and Lindauer 1971, Hoefer and Lindauer 1975).

Koltermann (1973) has found a similar rankorder between odours. He offered 17 different odours as potential learning signals. The rankorder was specific for *Apis mellifera carnica*, *ligustica*, *fasciata* and for *Apis cerana*. The following results are especially remarkable:

- (1) A relation exists between the specific rankorder and the *natural nectar crop* in the native area of the race or species. *Carnica*, *ligustica* and *fasciata* prefer Lavendel and Rosmarin, *A. cerana* has Rose, Orange, Fennel on the top of its rankorder. It is of special interest that Orange, nowadays one of the main crops of the italian bees, is not found at the top of the ranking list of this race. But oranges have only been cultivated for 300 years in the

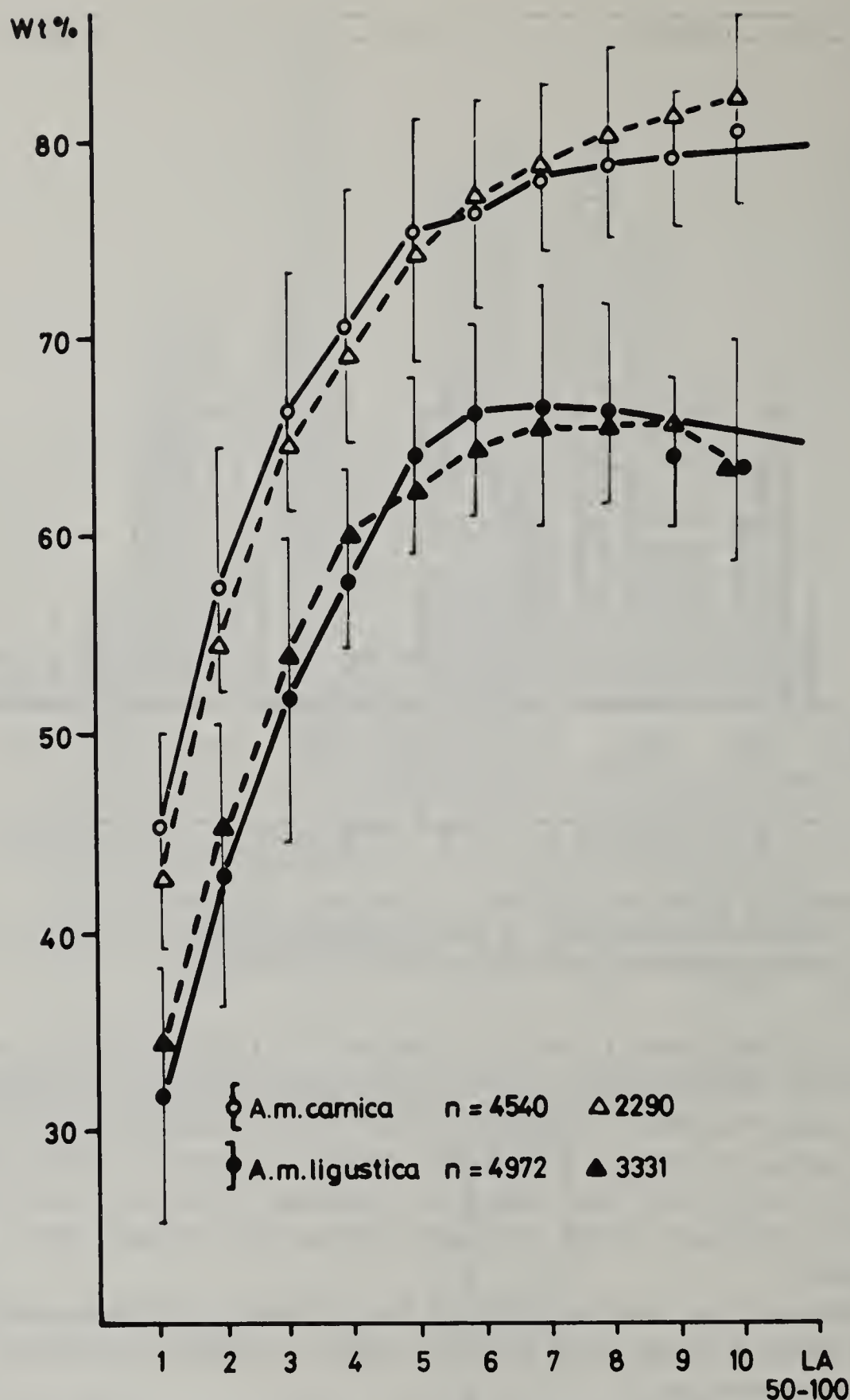


Fig. 11. — Food source is a black star in the center of a round table. In the test the star is offered on the edge of the table; pattern and location therefore compete as orientation cue. The ordinate gives the positive choices for the pattern. After each test bees are fed a new in the center on the black star (number of learning acts (LA) on the abscissa). *Apis mellifera carnica* prefers the location, *A. m. ligustica* the pattern of the food source.

mediterranean area — evidently in this short period the genetic learning disposition could not be adapted to the new environment conditions.

- (2) Hybrids of *A. carnica* x *A. ligustica*
and *A. ligustica* x *A. carnica*

In both cases present quite a new rankorder: 9 out of 17 odours range in another scale as they were in the parental generation. Further series of experiments have to clear up the genetic mechanism.

Relearning, Extinction and Forgetting. — Learning includes also relearning, extinction and forgetting. I will mention only one series of recent experiments: we trained the bees to search for food on the southern corner of a black star. To facilitate the orientation a black cylinder (10 cm x 20 cm) is posted at a distance of 20 cm. After 5 learning steps we remove the cylinder; training is continued now on the same setup but without the cylinder. The bees are unable for reverse learning; the correct decisions decrease to 25% after 17 new learning steps. However when we put back the cylinder after 16 learning steps, the bees start again to orient on the southern corner, but the new

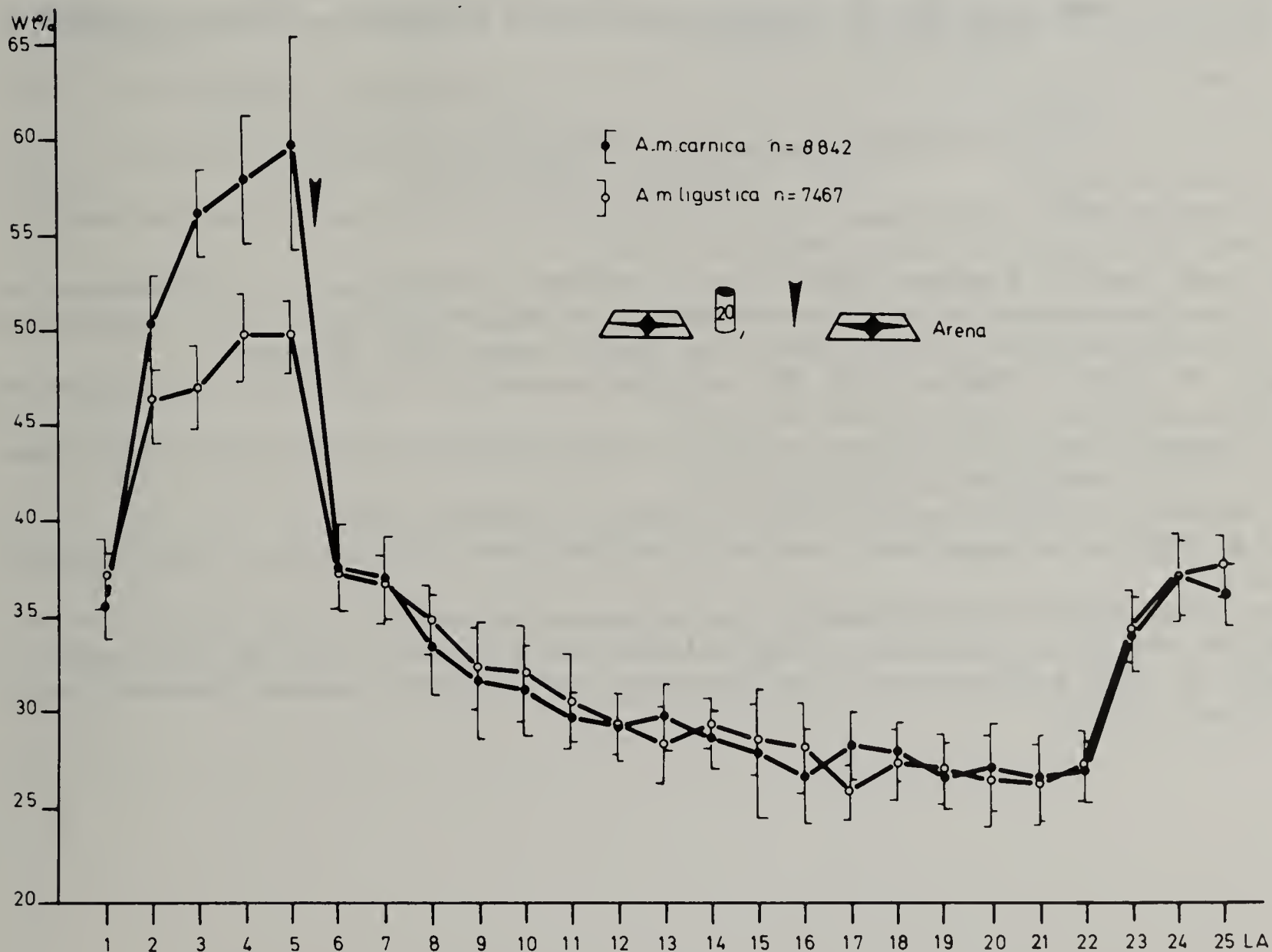
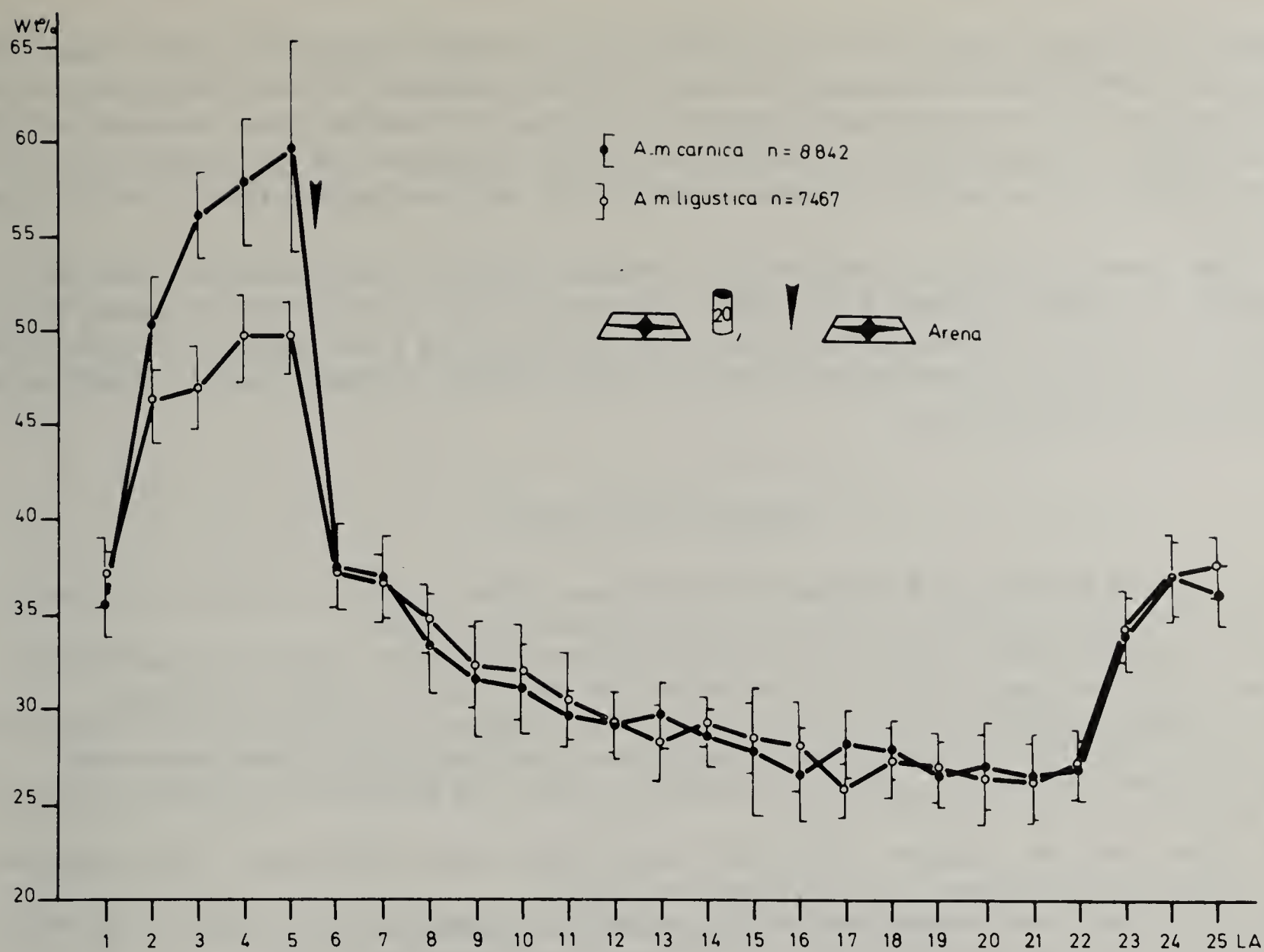


Fig. 12. — Food is offered on the southern corner of a black star. Beside the suncompass a black cylinder (20 cm high, in 20 cm distance gives an additional orientation cue). The learning curves in the first 5 learning acts again is race specific. After the 5th learning act the cylinder is removed, training in the following foraging flights without cylinder. Relearning starts only after 17 new trips.

learning curve continues with the second learning step of the early learning curve. That means: the information, stored in the first learning step was not forgotten; evidently this first learning step has its special function in the learning process. Opposite to the situation described above, relearning is easily possible when we change from a more difficult to an easier orientation task; i.e., when we first train *without* cylinder and we add this orientation mark after the sixth learning step (Hoefer and Lindauer 1976).

These results are again in correlation with "complex learning". If the learning set "black star" + "suncompass" + "black cylinder" is dissociated, relearning a similar situation without cylinder is very difficult and takes 16 additional learning steps or more. Relearning a new situation with *additional* orientation cues starts immediately, however. These findings probably lead to fundamental mechanism of a learning process.

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Section 8: Biological Control

Modern Achievements and Innovations in Biological Control

Organizer and Moderator: P.S. Messenger (USA)
(Ray Smith and Reese Sailer)

Modern Achievements and Innovations in Biological Control

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Division of Biological Control, Univ. of California, Albana

Introductory Remarks

It is with a sense of great inadequacy that I approach this task of making remarks which will serve as an introduction to this symposium. A proper introduction could have only been one in accordance with what Dr. Messenger, the organizer of this symposium, had in mind when he invited our distinguished panel of experts to participate. I have only a very general idea of what he had in mind, but I also know that Bud was very well aware of the advances taking place in biological control, that he stimulated those in search of novel approaches in this discipline, and that he knew that pursuing those advances and novel approaches was the surest way to avoid stagnation in biological control.

In the early days biological control was an art that must have developed as a result of shrewd observation of natural phenomena, observation that lead to the manipulation of entomophagous organisms. With the increasing knowledge of the agents of biological control, such as protelean and other parasites, predators, and pathogens; with a clearer understanding of host/parasite, prey/predator relationships, and of the role biotic mortality factors play in the regulation of populations, biological control rapidly reached the status of a scientific discipline.

In the last 10 or 15 years we have witnessed significant advances in the knowledge of strains of natural enemies better adapted to certain situations, of factors that determine specificity of natural enemies and of phytophagous insects, and of the role of hyperparasitism, thus making possible new approaches in classical biological control. In the field of natural control additional information has been gathered on the dispersal, both natural and induced, of insect pathogens; the discovery of kairomones has opened a new avenue to increase the efficiency of natural enemies; significant advances have been made on nutrition of natural enemies. Further investigation in these areas will certainly increase our capabilities to manipulate natural enemies in the field. The understanding of antibiosis, antagonism, and parasitism in plant pathogens has opened challenging possibilities in this new frontier of biological control.

These are some of the areas where new achievements and innovations in biological control have occurred, and all of us practitioners of biological control must become familiar with them, and incorporate them in our practice if we want to make of our discipline one of the indispensable components upon which crop protection programs are based.

We are very privileged to have with us a panel of recognized authorities in biological control who will discuss several aspects of this discipline. I leave this podium with great anticipation.

Biological Control of Agricultural Pests

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ABSTRACT

Several recent examples of classical biological control are discussed, including *Aleurothrixus floccosus* in southern Europe and California; *Unaspis citri* in Florida; *Epilachna varivestis* in eastern USA; *Promecotheca cumingi* in Sri Lanka; *Diatraea saccharalis* in Barbados; *Phthorimaea operculella* in Australia and parts of Africa; *Mythimna separata* in New Zealand etc. The present status of other aspects of biological control are reviewed briefly. The authors suggest that the practice of biological control should be given high priority in the pest management programs and that classical biological control is still under exploited.

Introduction

There are few rigid principles applicable to biological control to which quite conflicting results cannot be found, but certain patterns have emerged in the successes achieved against agricultural pests. While many of these successes can be attributed to the amount of effort put into the research, it can perhaps be generalized that the greater the stability of the environment of the target pest the greater the possibilities of control of say, an invasive species, would be. Thus biological control of orchard pests (and in forests) is more promising than that of pests of annual crops — particularly if the latter are scattered in small areas and change from season to season (Lloyd 1960). Further, biological control is usually of greater practical benefit (compared with the use of chemicals) in crops of low value, e.g., range pasture-land, than in high-priced crops, e.g., table apples, citrus or vegetables, where the final product has nowadays to be blemish-free, and where the use of often excessive chemical treatments is economically warranted. Classical biological control and inoculative releases usually cannot hope to achieve the very high degree of control of the pest required, although inundative methods or the use of insect pathogens *may* do so. However, the very successful biological control of olive scale, *Parlatoria oleae* (Colvéé) in California (Huffaker and Kennett 1966) and the successful control of *Therioaphis trifolii* (Monell) on alfalfa emphasizes the fact that there are exceptions to such generalizations (DeBach 1964).

Thus, in general, the agricultural pests most amenable to biological control are those of widespread (not necessarily complete monocultures) plantation crops, e.g., orchards, coconuts, sugarcane, cocoa, coffee etc., where the ecosystem tends to remain fairly stable from year to year, rather than those in areas of annual crops where there is a complete disruption of the environment each season. Some graminaceous crops in the tropics, e.g., rice, corn and to a certain extent sugarcane, present a pattern where there is often continuously present some of the crop (with seasonal peaks), and in any event the pests and parasites can often carry over on wild grasses. For practical economic reasons biological control is particularly valuable against pests of comparatively low value crops such as pastures where, apart from invasive or explosive “pests”, the ecosystem is again generally fairly stable and unaffected in calamitous ways by man, as are the ecosystems of annual crops.

As for examples of classic biocontrol which have occurred in the last 10 years or so we will describe briefly a few outstanding successes including examples of the utilization, in different areas, of natural enemies already proven successful elsewhere.

1. Woolly whitefly *Aleurothrixus floccosus* Maskell. — In the Mediterranean Basin of Europe the control of the woolly whitefly by *Cales noacki* Howard introduced from South America in 1970 has been a notable success although a satisfactory equilibrium between parasite and host has not been established in all areas (Anon 1976, Onillon 1975). Control, mainly by *C. noacki* and *Amitis spiniferus* (Brethes) in some areas of California has also been reported recently (DeBach and Rose 1976).

2. Citrus blackfly *Aleurocanthus woglumi* Ashby. — Following its successful introduction into Mexico the Aphelinid *Prospaltella opulenta* Silvestri has been introduced and has provided excellent control of citrus blackfly in Barbados (Pschorn-Walcher and Bennett 1967), in Jamaica (van Whervin 1968), in Long Island, Bahamas (authors' notes) and in El Salvador (Quezada 1974).

Very recently (1976) citrus blackfly was discovered near Fort Lauderdale, Florida. It would seem that attempts to eradicate it may not be successful. We consider it highly likely that one or more of the several readily obtainable parasites which have been so successful in controlling it in other areas could be introduced with every prospect of reducing *A. woglumi* in Florida to the status of a comparatively rare insect and by no means a serious threat to the citrus industry. Releases of *P. opulenta* have already been made and plans to introduce other species have been formulated.

3. Citrus snow-scale, *Unaspis citri* (Comstock). — In Florida the citrus snow-scale has been brought under satisfactory control since the introduction of *Aphytis lignanensis* Compere from Hong Kong and its establishment in 1973. Previously losses from this scale in Florida ranged from US \$20,000,000 to \$40,000,000 per annum (DeBach and Rosen 1976).

4. Rhodes-grass scale *Antonina graminis* (Maskell). — *Neodusmetia sangwani* (Subba Rao), the Encyrtid successfully introduced into Texas against the Rhodes-grass scale, from India, has now been similarly successful in Bermuda (I.W. Hughes, pers. comm.) and over large areas of Brazil (Costa et al. 1970).

5. The sugarcane scale, *Aulacaspis tegelensis* (Zehntner). — In Tanzania, the introduction (from Mauritius) and establishment of the well-known Australian Coccinellid *Lindorus lophanthae* (Blaisdell) produced a very worthwhile reduction in populations of the sugarcane scale *A. tegelensis* which previously caused serious losses to sugar production. Preliminary figures put this reduction of damage at 7,500 tons of sugar, or at least £750,000, per annum (Greathead 1975a).

6. Barnacle scale, *Ceroplastes cirripediformis* Comstock. — An Encyrtid, *Coccidoxenus mexicanus* Girault collected in Trinidad from *Ceroplastes floridensis* Comstock, was sent to Hawaii in 1967 where it has provided very good control of the scale *C. cirripediformis* on passion fruit (Davis 1974).

7. The Mexican bean-beetle, *Epilachna varivestis* Mulsant. — *Pediobius foveolatus* (Crawford) introduced from India, provides high levels of control of the Mexican bean-beetle in the USA if annual inoculative releases are made (Stevens et al. 1975).

8. The leaf-mining coconut hispid, *Promecotheca cumingi* Baly. — Another spectacular success has been against *P. cumingi*, which became established — probably on accidental introduction from Singapore — near Colombo, Sri Lanka (Fernando 1972 and Dharmadhikari et al. in press) in 1970. In 1971 CIBC was commissioned to obtain suitable parasites — and three species, *Achrysocharis promecothecae* Ferriere (which it seems possible might already have been in Sri Lanka), *Pediobius parvulus* (Ferriere) which previously had been very successful against *Promecotheca coeruleipennis* Blanchard (= *reichei* Baly), in Fiji (Taylor 1937) and *Sympiesis* (*Dimmockia*) *javanica* (Ferriere) (which had failed completely in Fiji) were liberated from December 1971. *Sympiesis* immediately became dominant, reduced the pest to an amazingly low level by mid-1972, and stopped further spread of the pest. *Pediobius* certainly, and *Achrysocharis* possibly are still present at extremely low levels. Had the outbreak *not* been confined it would certainly have spread over the whole coconut-growing area; the benefits have been estimated in Sri Lanka to be of the order of US \$40,000,000.

9. Sugarcane borer, *Diatraea saccharalis* (F.). — In Barbados, spectacular control of the sugarcane borer has been obtained by means of *Apanteles flavipes* Cameron from India together with a sudden increase of another parasite *Lixophaga diatraeae* Townsend which had been introduced

some years previously into Barbados but had remained for years at a very low population level (Alam, Bennett and Carl 1971; Simmonds 1972, 1976). The value of this control has been of the order of 4-8,000 tons of sugar per annum (over £1,000,000 per annum according to sugar prices). An increase in damage in 1976 but still below the economic threshold may be due to changes in sugarcane varieties. The cane variety B 63162 is being grown very extensively and this *may* prove more susceptible to *Diatraea* than some of the canes grown previously. *A. flavipes* was also tried in Florida at about the same time as it was released in Barbados (Gifford and Mann 1967); it is recovered more frequently outside the commercial cane area. Later it has been established in St. Kitts, Trinidad, Guadeloupe and Brazil. It is developing well in St. Kitts, but so far in none of the other areas has it built up populations to the same extent. It has also been introduced into Peru and Colombia; field recoveries have been reported recently in Colombia (J.D. Gaviria, pers. comm. 1976). From its spectacular achievements in Barbados it would appear to show great promise to have an important impact on cane-borer losses in the Neotropics. It will be of interest to see how it reacts in these widely separated areas, all of which have broadly similar ecological environments in the cane-fields, although naturally some differences in macro-climate. *L. diatraeae* has also been mass-bred and released in the USA as will be mentioned later.

10. Potato tuber-moth, *Phthorimaea* (*Gnorimoschema*) *operculella* (Zeller). — While progress in the control of potato tuber-moth by means of South American parasites — principally *Apanteles subandinus* Blanchard, *Orgilus lepidus* Muesebeck, *Campoplex haywardi* Blanchard and *Copidosoma uruguayensis* Tach. (or *koehleri* Blanchard) has been encouraging in Australia, it has not been continent-wide (Callan 1974). In Mauritius *C. uruguayensis* and *C. haywardi* have been established but potato tuber-moth is still a problem. Great success is claimed in Zambia where a projected total gain by 1980 of an estimated £235,380 for an expenditure of £15,363 has been achieved by the action of mainly *C. uruguayensis* and *A. subandinus*; *Bracon gelechiae* (Ashmead) *Temelucha* sp. and *Diadegma raoi* Gupta — are also established (Cruickshank and Ahmed 1973). *A. subandinus* has also gained a foothold in Madagascar, and *C. uruguayensis* and *Diadegma* sp. in St. Helena (authors' records). In South Africa *C. uruguayensis* and *A. subandinus* have been established and are now more abundant than the indigenous parasites (Watmouth et al. 1973).

11. The army-worm, *Mythimna separata* (Walker). — In New Zealand this army-worm, formerly a very serious pest of maize and also at some periods of pasture grasses, has been controlled by *Apanteles ruficrus* Haliday introduced into New Zealand from Pakistan. Although a race of this species already occurred as a parasite of cutworms in New Zealand it had little effect against *M. separata*. This situation has altered entirely since the release of the Pakistan strain in 1971. In 1974 and 1975 increasing control has been obtained and in 1975 New Zealand, previously an importer of maize, was able to export 80,000 tons. The benefits are estimated in New Zealand at some N.Z. \$10,000,000 per year (R. Cumber, pers. comm. 1975).

12. Stable fly *Stomoxys calcitrans* (L.). — In Mauritius, good control of *S. calcitrans* has been obtained for the last 10 years (in the drier areas only) by means of various parasites, the principal ones being *Pachycrepoideus vindemiae* (Rondani) and *Spalangia* spp. However, control of *Stomoxys nigra* (Macquert) has been ineffective, due no doubt to its different habitat — where larvae feed on rotting vegetation and hence they, and the puparia, are very scattered, not aggregated in dung as in *S. calcitrans*. In the USA the introduction of exotic parasites and predators in combination with the release and manipulation of native species has resulted in the development of a pest management industry for the control of synanthropic flies (Legner and Dietrick 1974).

Other successes over the last few years have involved the control of *Melanagromyza phaseoli* (Tryon) in Hawaii by means of the parasites *Opius phaseoli* Fischer and *O. importatus* Fischer from East Africa (Greathead 1975b) and of *Sesamia calamistis* Hampson in Madagascar by means of *Pediobius furrus* (Gahan) from East Africa. Attacks by *Spodoptera* spp., in Barbados (and subsequently in other neotropical areas) have been reduced by means of *Telenomus remus* Nixon originally obtained from New Guinea. *Erionota thrax* (L.) the banana-leaf roller, has been brought under control in both Mauritius and Hawaii with parasites originating from south-east Asia. In Peru *Selinaspis articulatus* Morgan one of the key pests of citrus has been controlled by *Aphytis roseni* DeBach and Gordh, a parasite introduced from East Africa (Bartra 1974). The whitefly *Aleurothrixus floccosus* in Tijuana, Mexico, and *Dialeurodes citri* (Ashmead) in California have been controlled by introduced parasites (DeBach and Rosen 1976). (For other examples see Simmonds 1969 and 1974, and DeBach and Rosen 1976).

Thus it is seen that even with classical biological control — as compared with the more modern concept of integrated control — there still continue to be very successful examples in a variety of agricultural crops on a world-wide basis. One *could* consider this the extreme of integrated control where the input of control measures other than basic biological control was negligible (other methods obviously may have to be used if the biocontrol breaks down for any of a variety of reasons or where other pests which are not under biological control are present).

Inundative and inoculative releases

Quite apart from so-called classic biocontrol, which consists of bringing into the pest situation exotic natural enemies to suppress it — often with the pest involved itself exotic and invading an ecosystem without its natural enemies — there is the method of inundative releases of natural enemies made at a critical time in the pest's life-cycle when populations of pest and natural enemies are low. The idea here, of course, is to suppress the pest population at the outset and prevent it rising to damaging proportions. This was attempted some 50 years ago using *Trichogramma fasciatum* Perkins (it was erroneously called *minutum* Riley at that time) in Barbados, British Guiana (now Guyana) and the southern USA, where there was great controversy as to whether beneficial results were obtained (for a review see Metcalfe and Brenniere 1968). *Trichogramma* was also used in the USSR as early as 1911 against codling moth (Dysart 1973), in India against sugarcane borers (Gupta 1951, Ramachandran et al. 1951); and for many years along with other parasites against *Nephantis serinopa* Meyrick, the coconut leaf-feeder, in Sri Lanka and southern India (Ramachandra Rao et al. 1948). In none of these earlier attempts were the results clear cut. In both California and Japan (and formerly in Switzerland too) there are commercial organizations which supply natural enemies for specific purposes — e.g., against scale insects in citrus, cotton pests, house-flies. It is now virtually standard practice to use *Encarsia formosa* Gahan against *Trialeturodes vaporariorum* (Westwood), *Phytoseiulus persimilis* (Athias-Herriot) against Tetranychid mites, in the relatively stable and controlled environment of greenhouses.

More recently this method, and inoculative releases of indigenous and introduced parasites, has been looked into more critically, for example, the experimental work undertaken against cabbage pests using several parasites (and viruses) in the USA (Parker 1971, Parker et al. 1970 and 1972) and also against maize stem-borer *Chilo partellus* (Swinhoe) in Pakistan using *Apanteles flavipes* (Mohyuddin 1976). Useful data is gradually accumulating and in addition to its application in greenhouses and by the citrus industry in California in both of which the method has been operative for some years, there are other areas where inundative releases are becoming as routine in practice as are spray programs. The mass-production of Trichogrammatids for release has now been almost completely automated in the USSR, where releases over hundreds of thousands of hectares are made annually (Dysart 1973, Klassen 1976); similarly in Mexico and Colombia more and more emphasis is placed on the production and release of *Trichogramma* for the control of a wide range of lepidopterous pests. In several of these programs the need for more critical data on their usefulness is recognized and attempts are being made to rectify this.

Attempts to automate the rearing of other groups of natural enemies have also proven successful. The methods developed for the mass-production and aerial release of *Lixophaga diatraeae* is an excellent example of what can be achieved where funding and modern technology are brought to bear on a specific problem (King et al. 1975). The mass-production of natural enemies for inoculation or inundative releases is an aspect of biological control with a considerable future, but one which needs further very careful experimental work to ensure that the claims of results obtained are valid and the method is economic.

Investigations on mites

The biological control of mites has received a certain amount of attention, particularly in connection with orchard crops in Australia, North America and Europe as well as in greenhouses as mentioned above. This has in general been in two aspects; the straight exploration for and introduction of predators (very often themselves mites) against pests, or alternatively the manipulation of predator/prey populations in glasshouses (as mentioned above) to control very effectively Tetranychids mites. This has been brought to a high degree of reliability, but there are perhaps two things to comment on here; firstly that the environment of a glasshouse is ideal for this

since as so many factors can be rigidly controlled, and it is a closed environment with very limited parasite or predator dispersal, and secondly that the predator which has been used almost exclusively is *Phytoseiulus persimilis*, a mite of Chilean origin. There seems no reason for thinking that other Phytoseiids (or other predaceous mites) might not be just as good or better than this particular species. There has, of course, been other successful biocontrol work involving mites, e.g., that on the cyclamen mite (Huffaker and Kennett 1956). Mass releases of natural enemies have also been attempted against mites on avocado (McMurtry et al. 1969). Investigations have also been undertaken in connection with mite control in orchards, with the production of pesticide-tolerant races of predaceous mites (Croft and Meyer 1973, Meyer 1974, 1975, Hussey and Huffaker 1976).

Microbial control

In the past few years microbial control has also developed rapidly and well, increasingly playing its part in integrated control programs, where the use of pathogens is far less disturbing to the ecosystems as a whole than is the use of chemicals. As this aspect will be discussed by one of the following speakers only this brief mention of it will be made here.

Other biological methods

There have been, and are being developed a number of additional methods of attempting to control insect pests which have met with varying degrees of success. These, because they involve the aspects of the behaviour of the pest species, have tended to be considered under the general heading of biological control, and are certainly less environmentally hazardous than chemical insecticide methods. As these are dealt with in greater detail by other speakers they will be mentioned only briefly here.

1. Autocidal methods involving the release of sterile males have proven to have a specialized, but so far limited, use in control of agricultural pests. Although there have been minor, usually very costly, successes in the eradication of fruitflies (Steiner et al. 1970) the only really major success with this method has been the eradication of screw-worm fly, *Callitroga hominivorax* (Coquebert) from Curacao in 1954, and from Florida in 1959, and its use in the continued suppression of this pest in the south-western United States, offsetting possible invasions from the south by continued mass-releases of sterilized males.

2. The use of sex-attractants has proven more useful as a tool to measure population fluctuations of agricultural pests than in providing any appreciable measure of control *per se*, and that of chemosterilants has so far proved too costly (and toxic) for widespread application.

3. As pointed out by Sailer (1976) insect growth regulators and toxic substances derived from organisms are beginning to find a place in practical pest management programs.

4. Anti-feedants, i.e., substances which deter feeding or are repellants, have been utilized experimentally (Kamel et al. 1970). While these may be of greater importance in the future they are still regarded to be in the experimental or developmental stage — also, they must become economically competitive with other methods of control.

5. It may be claimed that toxic substances derived from plants or animals which have long been in use for pest control, e.g., pyrethrum, derris, rotenone, are a form of biological control. However, these are used as straight chemical insecticides, as is the endotoxin produced from *Bacillus thuringiensis* Berliner, which has long been marketed as an insecticide. If *live B. thuringiensis* is present in the formulations then this would certainly be an example of microbial biological control.

6. Basic studies on parasite/host behaviour and relationships are leading to a better understanding of the factors involved in host-habitat location and host-location (Vinson et al. 1975, Vinson 1976). Lewis et al. (1972) have demonstrated that kairomones from the scales of its lepidopterous host attract *Trichogramma evanescens* Westwood into the host-habitat and result in a higher level of parasitism. Hendry et al. (1973) have reported the role of kairomones in the behaviour of *Orgilus lepidus* Muesebeck. Jones et al. (1971) and Vinson et al. (1975) have similarly isolated, identified and synthesized host-seeking stimuli for other parasites. Further work with kairomones, allemones and sex pheromones of both pests and natural enemies will undoubtedly advance our knowledge to the point where they can play a significant role in pest management strategies, particularly those substances which have no adverse side-effects to the ecosystem.

We are here, of course, straying from the path of previously accepted biological control, but all these developments stress the efforts being made to find adequate substitute procedures for the admittedly highly effective, but often environmentally hazardous, use of many of the chemical insecticides now available.

Plant resistance

The development of resistant crop varieties, often now referred to as a branch of biological control, offers a sound and very practical approach to the long range control of certain of our agricultural pests. Although almost completely insect resistant varieties of some crops, e.g., wheat against Hessian fly, have been developed, even a partial level of resistance can result in a marked reduction of the use of pesticides or need for other methods of control. For example, low to moderate levels of varietal resistance are considered worthwhile and the use of these has proved to be an unexpensive method of reducing both the amount of insecticide applied and the losses caused by *Diatraea saccharalis* to sugarcane in the southern USA (Hensley 1971, 1972). Yasumatsu (1972) has drawn attention to the combined use of resistant rice varieties and of natural enemies for controlling rice borers.

A recently developed method of assessing the level of resistance by a pentameter should make it possible for geneticists to screen for resistance to *Diatraea* in sugarcane variety selection programs (Martin et al. 1975). While the incorporation of pest resistance into crop varieties is obviously very desirable, and is in fact to-day, one of the more important aspects of plant-breeding, it should also be remembered that the production of varieties preferred to pests and by the grower and consumer because of their appearance, ease in harvesting etc., may entail unexpected loss of resistance. This may affect perfectly satisfactory biological or natural control adversely, and necessitate a complete review of a biological control effort — or the breeding back of resistance into the variety. This varietal breeding, traditionally in the botanical field of plant-breeding, falls rather outside the scope of the biological control worker and is another example of the necessity of interdisciplinary action in achieving good pest-management.

Biological control in pest management programs

We are still convinced that “classical” biological control by the introduction of and the natural development of field-populations of one or more natural enemies is economically by far the most satisfactory method of pest control. Let us say straight away that this is by no means always achievable, but that possibly successful results warrant the expenditure of funds on research on a far greater scale than at present and that the possibilities of achieving biological control of a far wider range of pests should be investigated. If only partial control is obtainable in a given situation then a prime aim of a pest management program should be to indicate those methods most suitable to complement it to obtain the desired level of control without the least deleterious effects on the natural enemies. It should be emphasized that whether the control is complete or only partial, classical biological control is self-sustaining, and after the cost of the initial investigations and releases there are few if any recurrent costs involved — this is in contrast with most other methods excepting the production of resistant crop varieties.

It is of interest to note that in several areas where pest management programs have been successful the role of classical biological control continues to be accorded high priority.

We will cite three examples.

1. In Peru, where pest management of cotton pests achieved early fame, this was based in part on the extensive use of *Trichogramma*, there have been subsequent attempts to obtain biological control of the key-pests of citrus — the woolly white-fly *Aleurothrixus floccosus* and the rufous scale, *Selinaspidus articulatus*. Parasites of both species have now been established and form the basis for further pest management with lessened reliance on chemical pesticides (O. Beingolea, pers. comm.).

2. In South Africa the introduction of scale parasites has simplified the citrus pest management program developed by Bedford (1976). The discovery of effective natural enemies to control the thrips *Scirtothrips aurantii* (Faure), which is now the key pest, would simplify the program further.

3. In Israel, as a result of the establishment of *Aphytis holoxanthus* DeBach against *Chrysomphalus aonidium* (L.) in the 1950's and as attempts to establish natural enemies of soft scales and mealybugs faced difficulties because of the present insecticide regime, groves in each citrus area

in which only selective pesticides are used have been set aside for the colonization of natural enemies.

Accordingly we feel that in most attempts at integrated control classical biological control, because of its economical nature, should be the basis — along with the encouragement of manipulation of indigenous natural enemies — into which other methods are “integrated” to provide requisite economic control.

From a health and environmental aspect it would certainly be better if the acceptable degree of pest control was markedly lower than it is at present. While at present a very high standard of blemish-free or undamaged fruit and vegetables is demanded this is usually only achieved by frequent, costly applications of pesticides. If such rather unnatural standards were not demanded integrated control methods could become simpler and less environmentally hazardous. Any such integrated control system, to be effective, particularly if it is obligatory to maintain present blemish-free standards has to be extremely well-monitored by personnel who are adequately trained and can with confidence recommend when and what action should be taken. We have seen an article (Anon. 1972) commenting on this which estimates that in the USA alone some 168,000 scouts and 11,000 skilled entomologists will be necessary. Without trained personnel integrated control is, in our view, rather a pipe-dream, and the employment of operatives on this scale, except under special circumstances of effective growers co-operatives, is rather restricted to certain high-value or highly organised crops over a limited area. We feel that much of the discussion concerning the advisability of integrated control rather overlooks this essential aspect. Without competent supervision detailed effective integrated control is impossible — and we then fall back on getting the best out of natural or biological control, disturbing these as little as possible by thinking more carefully of the effects of chemical pesticide programs. Alternatively, we virtually ignore all health and environmental hazards and go all out for blanket-spraying and 100% chemical control. This obviously cannot be afforded in the context of the environment, let alone of cost.

In all situations where integrated control is actually being *practised* or considered, the first efforts should be directed towards maximizing the effects of the natural controls by any means possible, and then adding where necessary a well-thought-out sparing use of chemicals to obtain the degree of control required. It follows that investigations to obtain maximum biological control are of basic importance to every pest management program. Legner and Dietrick (1974) have emphasised the valuable role of classical biological control in pest management programs against synanthropic flies and consider that the potential of classical biological control is still largely unexploited. Both DeBach (1974) and Sailer (1976) have drawn attention to the small percentage of crop pests against which introductions of natural enemies have been attempted. Even for most pests against which introductions have been made the possibilities of classical biological control have by no means been explored exhaustively.

In the past it has been made abundantly clear that research in this sphere results in prodigious economic benefits — without *any* environmental hazards — and we consider that there is no reason whatever why this method should not be expanded to cover many more situations.

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Microbial Control of Arthropod Pests

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The Editors of Bacteriological Reviews have recently pointed out that for microbiologists, 1976 is a year of centennials. In 1676, van Leeuwenhoek first saw his 'little animals', two hundred years ago Spallanzani was grappling with spontaneous generation, and just a hundred years ago Robert Koch isolated the anthrax bacillus.

Stepping outside of Science for a moment, I'm sure that everyone attending this Congress is aware by now, that 1976 marks another centennial – the bi-centennial of a political event that was undoubtedly a watershed in human affairs. The events celebrating the founding of the United States of America have added immeasurably to the many attractions of Washington and I am most grateful to the organizers for their kind invitation to participate in this symposium.

During the past week, there have been many papers delivered in the general area of insect pathology. These contributions have been quite specialized with emphasis on particular aspects of microbial control. In this Plenary session on Modern Achievements and Innovations in Biological Control the subject range is wide, involving use of parasitoids against agricultural and forest pest insects, biological control of weeds, the ecological basis of biological control, and, of course, microbial control. Briefly, I have prepared these remarks assuming that my audience would be largely of entomologists having only a general interest in current research on alternative methods for control of pest species. A parallel assumption was since this is a plenary symposium, the tone of my remarks should be general and the jargon of insect pathology avoided wherever possible.

My hope is to provide a personal overview of where we stand, rather than a detailed review since there are many excellent recent texts available on this subject (Burges and Hussey 1971, Huffaker 1971, Bulla 1973). I shall be referring to several host-pathogen systems to illustrate a particular point and you will find that many of these are drawn from the forestry scene.² I hope you will forgive my bias. In extenuation may I plead that the time is now past when a single individual could hope, in half an hour, to give a detailed account of current work in the agricultural, forestry and public health applications of microbial control.

May I begin with a few definitions. Biological control refers to the use of parasites, predators and pathogens to limit pest abundance. Microbial control is the use of pathogenic microorganisms, and includes viruses, fungi, bacteria and protozoa. The use of nematodes is also treated as microbial control although strictly speaking the nema are helminths. Burges and Hussey (1971) summarized the desirable attributes of a microbial control agent as:

1. Ability to spread among the pest population.
2. Ability to persist in the pest's environment.
3. Sufficient powers of search.
4. Ability to limit pest numbers below that causing economic damage to the plants when correctly introduced.

¹ Contribution No. 319

² As delivered, a large number of slides were presented; these are not included in this printed version.

5. It must be possible to produce or collect sufficient numbers of healthy specimens of the agent.

6. The agent should not destroy other biological agents unless it is able to take their place adequately.

7. It should provide predictable control.

When we consider microbial agents most of these constraints are still operative and some new ones appear. Heimpel and Angus (1960) discussed some criteria that seemed appropriate for bacteria being considered for use as microbial control agents; substituting pathogens for bacteria it read:

“An ideal pathogen would be highly virulent, able to breach the defences of the healthy feeding insect, and by some means bring about its death. The organism should cause death even when a small number are ingested and it is also desirable that the virulence be a stable characteristic. The pathogen ideally should have a dormant phase in its life cycle resistant to ultra-violet radiation and drying, enabling it to remain viable and virulent while exposed on the plant or in the insects’ habitat. Since some pathogens are extremely sensitive in the vegetative or growing phase, the insect pathogen should not readily discard its resistant form until ingested by the insect. The resultant disease should have a short incubation period, for if too long a period ensues between contact and death of the insect, the damage to the crop being attacked may be considerable. The pathogen must be reasonably specific for the insect pest it is being used against, and inactive against the host plant, useful parasites and predators, and most important of all vertebrates. It is also important that the microorganism be easy and relatively cheap to produce in sufficient quantity for widespread use. The product must be sufficiently stable to permit production and storage before the growing season begins”.

Today we might make some changes in that prescription but most of it would still be pertinent. When it was first stated, it was suggested that this was a very rigorous set of constraints that would exclude many natural pathogens from consideration, and this has proved to be the case. The extent to which it has been possible to meet, or to modify some of these limiting factors or constraints is a reflection or measure of achievement.

The known microorganisms affecting insects include about 300 viruses, nearly 100 bacterial species, more than 100 species of fungi and about 75 species of protozoans. Many species of nematodes have also been isolated from insects. Up until the end of World War II, in spite of several attempts to use microorganisms against pest insects, little success was achieved. Progress in the post-war period has been substantial and is due, in part, to several new factors.

The first was the development by the pharmaceutical industry of mass fermentation methods and equipment for production of antibiotics and other biologicals. Thus, when the potential of *Bacillus thuringiensis* as a microbial control agent was realized, facilities were available for producing it in quantity. Of equal importance was the accumulated expertise in such matters as the automatic measurement and control of oxygen levels, pH, suppression of bacteriophage contamination, harvesting and stabilization. As a result *B.t.* came on stream very quickly because post-war interest in antibiotics had created an applicable technology that was readily available.

A second contributing factor was the development of tissue culture techniques. In the thirties Carrell had succeeded in maintaining part of a living organ outside of the donor animal. Others then went on to adapt other kinds of cells, and by 1950 a wide range of mammalian and avian cells had been successfully cultured. Progress in culturing insect cells went relatively slowly because the work was carried on as a continuing study in only a few centers, and with literally only a corporal’s guard of investigators, few of whom were adequately funded or equipped. Mainly at the urging of insect virologists this changed and today a variety of insect cell lines are available.

The importance of this development is that pathologists dealing with obligate pathogens (i.e., those that grow only in living cells) can make observations and conduct experiments under highly controlled conditions, and in ways not possible in the intact host animal. Thus, by use of tissue culture we now know by direct observation much more about pathogen development as an on-going dynamic process. This knowledge has been extremely useful.

Another important benefit of tissue culture is that obligate pathogens of seasonal insects can now be studied “out-of-season”, i.e., on a more or less continuing basis. Previously, with temperate-zone univoltine defoliating species there was a hectic all-too-short experimental period followed by a lengthy down-time. In order to increase the experimental period some species were brought out of diapause early and raised (with heavy losses) on forced foliage but the cost in time and effort was prohibitive. A corollary benefit of tissue culture is that short-lived pathogens can now be cultured on a continuing basis.

At the present time considerable effort is being devoted to study of mass-culturing methods. Briefly, the goal is that susceptible cells will be produced in large volume equipment, infected with the desired pathogen and harvested at the optimum-yield time. This would make possible the production of substantial amounts of a particular pathogen with minimal amounts of extraneous host tissue. Many formidable technical problems must be solved before mass culturing of obligate pathogens is realized and the economics of the approach is also an imponderable. However, the goal is a highly attractive one, and thought by many to be achievable.

As we attempt so-called molecular engineering experiments, tissue culture methods will be indispensable in studies of virulence enhancement, relative vigour, effects of external factors and so on. Although it may seem odd to put insect tissue culture under the microbial control umbrella, the needs of insect pathologists played a major part in providing impetus and justifying the necessary manpower and money needs.

Ranking equally with tissue culture as a new factor in pathogen production, is the rearing of insects on artificial or synthetic diets. This relatively new method has been utilized very extensively in the rearing of lepidopterous defoliators on semi-solid diets and a surprisingly large number of species are now reared on a routine basis. They include such important forest pests as the tent caterpillar, the gypsy moth, the spruce budworm, and tussock moths. A wide range of agricultural pests are also reared in this way.

Such mass rearings are the usual source of virus preparations used in field experimentation. Substantial quantities of budworm, tussock moth and gypsy moth viruses have been already produced and used with promising results. In the agricultural field a commercial preparation of a baculovirus against *Heliothis zea* is commercially available. Just recently a baculovirus affecting the Douglas-fir tussock moth was registered; it has proved effective in experimental aerial applications in the U.S.A. and Canada.

In virus preparations prepared by use of mass reared larvae, a substantial quantity of extraneous host tissue is unavoidably present. However, the amount of contaminating saprophytic microorganisms is reduced by lyophilizing infected larvae at point of death; this yields a stable product easily macerated and these methods are equally adaptable for production of protozoans, fungi and some nematodes. In many respects, animals produced on synthetic diet are more satisfactory than field collected material since other diseases and parasites are not present. In mass rearings, hatching and development are predictable and so the workload of handling, infecting and harvesting can be dealt with on a planned basis.

Again, may I stress that I am aware that use of synthetic diets is not the exclusive domain of insect pathologists but I do believe that our needs, and the knowledge we brought to bear on control of contaminating microorganisms was an important part of the development of those methods.

Microbial control of insects has also been the beneficiary of methods and procedures developed for the application of chemical insecticides. This is perhaps ironical, for part of the support for use of microbials stems from growing disenchantment with side-spectrum biocides. The practitioners of chemical spraying have developed an extensive and effective array of emulsifiers, stickers, wetters and other additives, and these have proved to be exceedingly useful in preparing formulations of microbials. Equally useful has been the equipment and procedures developed for both ground and aerial spraying. In the case of forest spraying the existing methodologies for mixing, applying, and deposit assessment have been adopted with relatively minor changes. An important departure has been the need to include appropriate sunlight protectants because *B. thuringiensis* spores, viruses and other agents are inactivated by direct sunlight. A wholly effective protectant is not yet available and much work has been devoted to evaluating compounds and developing encapsulated products.

The wisdom of this borrowing operation has been questioned by some who argue that we have been attempting to use microbials as if they were simply another kind of chemical, looking for quick knockdown and foliage protection at high pest densities. It is argued that a more effective strategy would be, in the case of pathogens that have ability to persist and spread, to introduce the pathogen earlier in the pest infestation cycle. A new mathematical model developed for evaluating spruce budworm management strategies suggests that even a modest increase of the mortality sustained in the early years of an outbreak would profoundly affect the buildup of this particular pest. If we have been guilty of too eagerly taking over an existing technology and thus neglecting to develop more appropriate use-strategies for microbials, there are indications that this is now recognized.

Turning now to specific diseases, many of them are well beyond the bench stage and some are, in fact, commercially available. Just about 20 years ago *B. thuringiensis* was first touted as a

potentially useful agent for use against Lepidoptera. The commercial availability of *B. popillae* which causes milky disease in the Japanese beetle predates *B.t.* but its market penetration is limited by availability of the product which is produced by a method that does not lend itself easily to scale-up. *B. thuringiensis* is very easily grown saprophytically, and formulations of it are available under a variety of trade names both in North America and Europe. For protection of certain kinds of vegetative crops it is the insecticide of choice, and because of its safety and specificity has some definite advantages in forest use especially where conventional insecticides cannot be used. *B.t.* is a success story, for it is a microbial preparation that is commercially available, fully competitive in terms of price, completely safe and effective when properly used. There are many pest problems where the potential of *B.t.* should be further investigated.

Although several *B.t.* formulations have been tested experimentally against a number of forest pests, the results have often been variable. It has been suggested that further refinements in application technology are required (Harper 1974, Anon. 1976).

Next in order of availability or stage of development are the baculoviruses (nucleopolyhedrosis viruses). Those attacking Tenthredinid larvae (commonly called the sawflies) are especially virulent and spread very easily because sawfly larvae are colonial. Prof. Southwood mentioned in his plenary paper the classic example of microbial control: the European spruce sawfly (*Diprion hercyniae*) in Eastern Canada. Following the virus epizootic that reduced the outbreak to innocuous levels, the populations have remained at a very low level for the past 30 years.

Reference has been made to a commercial formulation of baculovirus for control of *Heliothis* spp. and an experimental product now registered for use against the Douglas-fir tussock moth. Viruses affecting some sawflies have long been used on a "cottage-industry" basis by forestry plantation managers. A virus affecting the rhinoceros beetle, *Oryctes rhinoceros*, (a pest of palms) has been used with great success for control of this pest. Mixtures of chemicals and viruses have been tested with promising results in experimental trials in the U.S.S.R. and Canada.

In the past, there have been only a few attempts to utilize protozoans as microbial insecticides. Recently, in the U.S.A., branbait formulations of a *Nosema* sp., gave successful control of grasshoppers over 10,000 acres of rangeland. In Canada, it has been shown that levels of *Nosema fumiferanae* infection in spruce budworm can be increased by applications of spores of this protozoan.

Many species of *Entomophthora* have been isolated, and the hosts include a wide variety of insects. Species of this kind of fungus are important determinants of insect abundance, and in some cases are thought to be key factors in terminating insect outbreaks. Good examples are provided by the tent caterpillar, the hemlock looper, certain aphids and a wide variety of agricultural pests. Substantial progress is being made in the development of liquid fermentation techniques for mass production of some *Entomophthora* spp., long thought to be obligate pathogens. Progress is also reported in studies of the factors inducing resting-spore germination. Preparations of other entomopathogenic fungi, notably species of *Beauveria* and *Hirsutella*, have been tested in field applications against a variety of pests.

Although commonly thought of as plant pathogens, many species of nematodes attack insects and much natural mortality undoubtedly is due to this kind of parasite. Our knowledge of this kind of association is at best fragmentary, but much work has been done on mosquito larvae and bark beetles. A species of meremithid is now available commercially (Skeeter Doom^R) for control of some kinds of mosquitoes. The product has been introduced only lately, but high levels of infection and mortality have been achieved in some applications.

These examples of current work in the development of microbial control agents are only a small part of what could be cited if a full list was to be presented. However, they do indicate that work is proceeding successfully in many centres in North America, and no less so abroad, on a wide variety of potentially useful agents. In a recently announced program, the World Health Organization plans to expand studies of microbial control of certain insect vectors of human diseases. This is a program of great importance, and if successful will help reduce much human misery and suffering.

In closing, may I make reference to what is becoming recognized as an additional benefit of microbial control methods. Most chemical pesticides are produced in those countries where there is available the expertise and sophisticated equipment of the petro-chemical and associated industries; in short it is based on "high-technology". Many developing countries with severe pest problems simply cannot afford such products. Since some microbial preparations can be produced with relatively simple equipment and natural starting products (as opposed to complex organic compounds), control

based on microbial products may provide a technically feasible, and economically acceptable alternative.

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Biological Control of Weeds: from Art to Science

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Biological control is the use of an insect, pathogen, vertebrate or other living organism to control a pest. It is an old method of controlling weeds but its development has been slow, largely I believe because projects tend to have been done empirically with relatively little attention being given to putting the method on a scientific basis. Thus, today many of the decisions are still a matter of intuition rather than conscious analysis. Still the method has evolved and the purpose of this paper is to identify some of the constraints that have been overcome and some that face us today.

The first constraint was the failure to recognize the potential of insects or other organisms for controlling weeds. Modern biological control arose by serendipity, in 1795 when a cocheneal insect from Brazil was introduced into India for the purpose of dye production. This was not successful; but the insect spread rapidly onto the *Opuntia vulgaris* that had gone wild. The result was to control cactus in North India and practically eliminated it in the south (Rao et al. 1971). There are records in 1863 of cocheneal distribution in India specifically for cactus control. The example was set in India but it was the Australians who enabled others to use the method by reporting the results (Tryon 1910, Johnston and Tryon 1914).

Biological control had similar but independent origins in Hawaii. The tropical shrub *Lantana camara* which was introduced as an ornamental, had spread by 1900 to occupy large areas of range land. The shrub rapidly re-established itself after clearing so there was no practical method of control, although an accidentally introduced scale insect (*Orthezia insignis*) was observed to damage it. The ranchers took the obvious courses open to them: they complained publically, and privately they distributed the scale insect even though it was known to be undesirable. I imagine that it was a pretty desperate government that sent an entomologist, Prof. A. Koeble to Mexico to collect other insects that would feed on *Lantana*. He went in May 1902 and sent back numerous species of insects that he felt intuitively would not attack desirable plants. These insects were released in Hawaii and either satisfied or disillusioned the ranchers as Prof. Koeble returned to his work on sugar cane leaf hoppers in December of the same year (Perkins and Swezey 1924). This project was done incredibly quickly and cheaply but this approach has the drawback that it depended on the intuition of one man.

The significance of the *Lantana* project does not seem to have been recognized at the time as the contemporary reports (Perkins 1902, 1903a, 1903b, and 1904) were largely for local consumption. However, word did reach Australia so both the project on *Lantana* in Hawaii and on prickly pear in India had a direct bearing on the subsequent development of biological control.

Some *Lantana* and prickly pear insects were introduced into Australia in 1914 (Wilson 1960). The war interrupted the program but by the end of it, biological control had obviously received considerable thought. The main constraint was the risk to desirable plants from the introduced insects. This problem was solved by showing that the insect starved when confined to a wide range of economic plants. The same type of test is used today but the emphasis is on determining the limits that the agent will accept rather than on what they reject. Wapshere (1975) has dubbed this the centrifugal-phytogenetic approach as the tests start with plants closely related to the weed host and then proceed to more distantly related ones. In addition the reasons or the basis of the host specificity are investigated. The gall-fly *Tephritis dilacerata* is restricted to perennial sow-thistle because for gall development egg hatch must coincide with the rapid growth of the flower buds (D. Berube, unpubl.). The fly cannot cope with different sets of cues and synchronisms and the annual

sow-thistles with a faster developmental rate are attacked by a sibling fly that accepts small buds and has a shorter egg incubation. With this type of testing the hazards of biological control are largely eliminated, although as the testing represents about two scientist years for each insect, it has added a cost restraint.

The next question is what type of weed problems are most suitable for biological control. The Australians in the 1920's clearly regarded introduced weeds dominating large areas of range or other relatively undisturbed sites as the most suitable targets for biological control. About one third of the land mass of the U.S. is classified as pasture that cannot be improved by cultivation (Klingman and McCarthy 1958). The area is large enough that its occupation by introduced weeds affects agriculture, recreation and wild-life on a continental scale. Chemical and mechanical control are clearly uneconomic so the problems of this type fall to biological control by default. Indeed Cussons (1974) suggested that only weeds that are difficult to control by conventional means and are of serious economic importance are suitable subjects for biological control. This approach is too simplistic. The best method is the one with the most favourable cost-benefit ratio without undesirable side effects. The costs of biological control are relatively easy to determine. The problem is comparing the benefits from biological and chemical control of weeds as they are not quite the same. The ideal herbicide suppresses all plants except for the crop while biological control merely suppresses a single plant species in the community. Both effects are desirable depending on the situation. The suggestion proposed by the Mrak commission in the United States that the chemical industry should be subsidized to develop herbicides for single plant species (Klingman 1975) is to lose the special advantages of both methods. Such a herbicide will require to be applied annually in a treadmill-like fashion, have a development cost about ten times that for biological control and still only control a single species.

The effects of biological control were shown following the release of the beetle *Chrysolina hyperici* on St. John's wort in an Ontario meadow (Table 1). The St. John's wort was reduced to a negligible density, the forage species increased by about one third but the biggest increase was in the production of other weedy species such as *Potentilla*. If the object were to reduce the abundance of a toxic pasture weed, the project was highly successful. However, if the object were to increase forage yield, the project was only partially successful, although probably with a more favourable cost-benefit ratio than could be achieved chemically in this situation.

Table 1.—Effect of releasing *Chrysolina hyperici* in 1969 on an ungrazed field near Picton, Ontario.

Year	Dry weight of foliage per m ² in the first week of July			
	St. John's wort	Forage spp	Weedy spp	Total Yield
1970	91.4 g	65.7 g	16.5 g	173.6 g
1971	12.0 g	60.6 g	30.3 g	102.9 g
1972	0.2 g	99.0 g	66.0 g	165.2 g

There are many plant species such as leafy spurge or wild garlic where the prime concern is the suppression of a single plant species and there is little concern about what replaces it. Such problems are nearly always suitable for biological control if the acreage is large enough to justify the initial investment.

The easiest and cheapest biological control is against a weed on which the method has worked successfully elsewhere and generally the same agent should be used. For example, following the Australian successes against prickly pear, this weed was successfully controlled in Indonesia, New Caledonia, East Africa, South Africa, Nadagaster, Mausritius, Celebes, Java and other places. Similarly, following the work on St. John's wort in Australia in the 1930's the weed was controlled on 2 million acres of range land in California in 1944. Canada followed suit in 1952 with the release of the insects in British Columbia and then later in eastern Canada. The problem was

chosen, not because of the importance of the weed which was relatively small but because in view of the previous studies, biological control offered a solution that could be applied quickly and cheaply. In most release areas *Chrysolina hyperici* or *C. quadrigemina* have reduced and maintained the weed at about 2% of its former density (Harris et al. 1969).

Introduced weeds that are monopolistic over large areas of range or other relatively undisturbed areas are always good targets for biological control. Prickly pear, against which the Australians achieved such spectacular success, was a weed of this type with some stands collapsing 18 months or so after introduction of the moth *Cactoblastis cactorum* (Wilson 1960). They achieved partial success against St. John's wort but against several other weeds of this type their success was less satisfactory (Wilson 1960). However, I do not think the reason for their failures was their choice of the target weed. The following are some Canadian problems of this type: St. John's wort, although because of biological control you will not see large massed stands in the interior of British Columbia; diffuse knapweed, which occupies about 26,000 ha and spotted knapweed another 3,500 ha in British Columbia (Watson and Renney 1974); plumeless thistle in Ontario and its close relative nodding thistle in Saskatchewan, Manitoba, and Quebec tend to form stands impenetrable to man or beast; leafy and cypress spurge which tend to be monopolistic and are difficult to control by other means. Suitable problems are not restricted to the new world: large parts of the Rhine valley are dominated by introduced goldenrods (*Solidago* spp) which are far taller, healthier and denser than any I have seen in North America where they are indigenous. Introduced goldenrod is also a problem in Japan. The prime object in all these examples is the control of a single undesirable plant and it matters little to the success of the project what species replace it. Indeed, it is desirable if a complex of plants replaces the monostand of the weed.

The third category of biological control targets represents an extension of the method to both native weeds and weeds of cultivated land. There is no need to exclude native plants when the American elm which is indigenous to eastern North America provides such a conspicuous example that native plants are vulnerable to introduced agents. Similarly, the use of a native pathogen against a native weed, i.e. northern joint vetch in the United States, demonstrates that the method can be effective against specific problem weeds in cultivated crops (Daniel 1973). I suggest that wild oats, the number one weed problem in Canada would be amenable to biological control by indigenous pathogens.

Some biological control agents such as the gall nematode, *Paranguina picridis* which is used in the USSR against Russian knapweed, can be applied like a granular herbicide on extremely small stands of the weed and the nematode. If kept dry, it has a shelf life of ten years or more (Watson 1976).

Thus, contrary to earlier opinions, biological control is quite versatile in the type of problem to which it can be applied. The main constraint is that each agent can only be used against single weed species and so can only be successful when there is some benefit in controlling one single weed species in a plant community.

The Australian policy against prickly pear was to introduce as many biological control agents as possible. They introduced 51 species of which 5 were effective (Wilson 1960). Today as the host testing of each agent represents about two scientist years, a project of this size would be a godsend to unemployed entomologists but not to austerity minded governments. The obvious solution is to eliminate the ineffective agents before starting the host testing procedure. The common reason for failure that can be found in literature is that the ecological needs of the insect are not met by the release area. This has happened with *Chrysolina varians* in Canada (Harris et al. 1969). Some other releases have failed because the agent encountered heavy predation or even because diseased stock was imported and the disease spread through the culture in crowded conditions of the laboratory. These built-in checks, which are the result of continuous selection (Chitty 1967) to prevent undue pressure on the host, will often start to operate at levels well above the economic threshold for the weed. For biological control to be effective there must be a breakdown in the normal homeostasis of the plant-parasite system. This can be done by stress on the plant and/or by ensuring that the agent is without its normal checks.

There will have been least opportunity for the control agent to have developed a sophisticated self-regulating system if it is normally well controlled by competitors or parasites of its own. Thus, effective control agents are likely to be those that feed gregariously, as they lack mutual antagonism, and those that are heavily parasitised or are displaced by competitors in their native area. In other words an *r*-rather than a *k*-strategist is required. This was the basis on which the seed-weevil,

Rhinocyllus conicus, was selected for the biological control of nodding thistle in North America. In Europe, *R. conicus* eggs are heavily parasitized by a specific trichogrammatid (*Pterandrophysalis levantina* Novitzky) and there are several larval parasites as well. Also *R. conicus* is displaced by two species of lepidoptera (*Homeosoma nebulellum* and *H. binaevellum*); a trypetid (*Urophora solstitialis*) and two weevils *Larinus sturnus* and *L. jaceae*. *R. conicus* survives in spite of this heavy competition by virtue of its fecundity and its ability to distribute its eggs on most of the nodding thistle heads. At Mulhouse in the Rhine valley, Zwoelfer (1973) found that 98.2% of the heads had *R. conicus* eggs on them; however, because of parasites and competitors only 31.5% of the heads produced pupae or adults. On introduction to Canada, the weevil has maintained its habits but in the absence of the check by parasites and competitors, its population has increased beyond densities found in Europe. Thus, at Findlater, Sask. in 1975, 92% of the heads contained mature weevils and this total is expected to continue rising.

Some insects have become established in good numbers but remained ineffective as biological control agents as their time of attack or the type of damage done by them was inappropriate. Generally speaking biological control, like mechanical weed control, is most effective when the damage is inflicted at frequent intervals through the growing season. For example, the tingid, *Teleonemia scrupulosa* introduced into Hawaii in 1902 defoliated *Lantana* in the summer but in the equitable Hawaiian climate the shrub recovered in the winter. The solution adopted around 50 years later was to introduce three species of leaf-feeding *Lepidoptera*, *Catabena esula* (Druce), *Syngamia haemorrhoidalis* Guenee and *Hypena striga* F., that were active in the cooler winter months. The four species complex has resulted in excellent control in the drier areas (those with less than 100 cm of rain a year) (Andres and Goeden 1971). More recently, two leaf-feeding beetles *Octotoma scabripennis* Guer and *Uroplata girardi* Pic were introduced as they were out of phase with all the other defoliators (Harley 1969b) as well as a stem boring beetle *Plagiohammus spinipennis* (Thoms.) (Harley 1969a). Thus, one strategy for the selection of effective insects is to choose species or combinations of species that attack throughout the growing season. This is the only strategy likely to succeed where there are no severe climatic or ecological stresses on the weed.

Where there are climatic stresses such as frost or drought, plants are vulnerable to damage during or at a critical time before the stress. For example, if alfalfa is to overwinter in a cold climate it should not be cut or grazed 6-7 weeks before the first killing frost (Smith 1964). A biological control example of this is provided by the cinnabar moth. This moth is established on both the east and west coasts of Canada and in both regions it defoliates the weed annually when it is in full bloom. In British Columbia, this occurs around mid June whereas in the later spring of Nova Scotia defoliation is delayed until around mid July. This difference is enhanced by an earlier onset of winter and the availability of moisture for summer regeneration. Thus, the weed at Truro, N.S. has 47 to 94 days in which to replenish its reserves before winter whereas at Nanaimo, B.C. the period ranges from 98 to 122 days (P. Harris et al. unpubl.). The result is that in many years in Nova Scotia there is a complete mortality of the defoliated plants and the density of the weed in the release fields has dropped to 0.01% of its former density (P. Harris et al. unpubl.). In contrast in British Columbia the defoliated plants invariably survive and the density of the weed has changed little since the introduction of the moth. It would appear that an effective agent for British Columbia would have to defoliate much later than mid June and preferably would attack throughout the growing season.

It is difficult to prejudge the merits of any prospective biological control agent. However, one must start working with one or another species and in view of the cost of the screening tests, I think it is essential that the selection process be put on a rational and scientific basis at the outset. Two approaches have been suggested. They both have drawbacks but at least it is a start. I (Harris 1973) assigned scores to various criteria such as fecundity, the position of the agent in its competitive hierarchy and other criteria that contribute or detract from the potential of the agent for biological control. The system is easy to apply and focus attention on the weakness of the agent but the criteria are partly subjective. The approach used by Wapshere (1976) was to create infestations of the weed in its country of origin and then observe the agents that contribute most to its control. It was on this basis that the rust *Puccinia chondrillina* was selected for the highly successful biological control of skeleton weed in Australia. The difficulty with this approach is that it is difficult to determine what the various phytophagous agents can do without their parasites and competitors. Also, for logistic or political reasons, it may not be possible to work in the climatic analogue of the release area, so that the observed result is not necessarily appropriate. I suggest that a combination of the two approaches be used, if possible.

The fifth constraint to the scientific advancement of biological control is the assessment of the impact of the agent on the weed. Without proper assessment there can be no feed-back for the improvement of future attempts. Normally failures are more instructive than successes but unfortunately almost all the attention is given to the successes. Success generates support for future attempts but it should be evident without a detailed study where there is a marked decline in the weed over a large area.

Biological control will not have made the transition all the way to a science until it is possible to accurately predict its impact on the weed. At present this is only possibly when using an agent that has been tried many times before such as *Cactoblastis cactorum*. With a relative new agent such as *Rhinocyllus conicus* we can predict with fair accuracy that it will survive and increase to destroy a considerable number of nodding thistle seeds. However, we must wait to determine if it can destroy enough seed to reduce the abundance of the thistle and if it does what effect this will have on the distribution pattern of the thistle. It has sometimes been assumed that the control agent will produce a contraction of the weed away from its fringe area but permit it to survive in its optimum habitat. This has been diagrammed by Wapshere (1971) and is what happened to the sweet chestnut (*Castanea dentata*) following the introduction of the chestnut blight in North America. However, the converse may happen if the agent has a narrower distribution range than its host. Thus, the sunloving St. John's wort has, according to Huffaker (1957) appeared to become a shade-loving species in California as the beetle *Chrysolina quadrigemina* practically eliminated it in the sun but hardly touched the rather scraggly plants growing in the shade. McMinn (1975) suggested that this has happened on a grand scale with *Pinus radiata* and Sitka spruce. He suggested that the former species is restricted to a narrow coastal belt in California as this is one of the few places where the red band disease *Cirrhia pini* is uncommon. The disease persists in a less damaging form on other pines in the moist and more productive habitats for *P. radiata*. Similarly, he suggested that Sitka spruce is restricted to the coastal fog belt of British Columbia and Alaska because the region is too cool for the survival of the weevil *Pissodes sitchensis*.

Prediction will probably involve the use of computer simulations to reveal the vulnerable points in the life cycle of the weed. In my opinion the lack of attention given to the ecology and population dynamics of the weed before selecting an agent is the major deficiency in the present application of biological control. The technology is available although its application may require a team rather than the traditional individual approach. With accurate prediction, biological control could be safely used against weeds for which a certain threshold population is desirable. Native plants such as big sage, *Artemisia tridentata*, in western North America and mesquite, *Prosopis juliflora*, in the southwest are examples of this kind of problem. At present, biological control is largely restricted to weeds for which any density below the economic threshold is acceptable. Also, the lack of predictability tends to result in an overkill strategy as several agents, each of which could control the weed, are usually introduced.

Thus, the present status of biological control is that it is a safe and useful method of controlling individual species of noxious weeds but it is slower and more expensive than necessary because of the empirical element still involved.

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Section 9: Medical and Veterinary Entomology

Changing Patterns in the Transmission of Arthropod-Borne Disease

Convener: RONALD A. WARD (USA)

The Ecology of Chigger-Borne Rickettsiosis and Murine Typhus — Changing Concepts and Epidemiology¹

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ABSTRACT

Our concepts of the ecology of chigger-borne rickettsiosis (scrub typhus) have changed considerably since the days in World War II, when this disease was one of the major medical problems in the armed forces in the Asiatic-Pacific area. Instead of being restricted to scrub terrain in tropical or subtropical areas or climes, the infection has been found endemic in a far greater variety of habitats, over a broader range, and under much colder conditions than had ever been expected. It is now known in environments as diverse as the equatorial rainforests of Malaya, the semi-deserts and montane deserts of Pakistan and the subarctic reaches of the high Himalayas, and cases are now recognized as occurring in the winter months in Japan. All endemic foci are characterized by the following features: (1) Chiggers (trombiculid mites) of the *Leptotrombidium deliense*-group, infected with *Rickettsia tsutsugamushi*, (2) Wild rats of the subgenus *Rattus*; (3) Secondary vegetation, instead of a uniform climax-type, and (4) ecological changes in the microhabitat, whether they be cyclical or periodic; abrupt or gradual.

The extreme diversity of types of endemic terrain reflect the geological and ecological history of the various areas. Thus, foci vastly dissimilar in appearance today may have been a continuum in the past, and the pockets harboring *R. tsutsugamushi* infection apparently represent relict faunae or inhabitants of ecological islands which have survived despite vast climatic and topographic changes, such as those wrought by the upthrust of the Himalayas and the creation of arid lands in the rain-shadow. However, the converse is also true — areas that appear homogeneous and confluent regarding biotypes may actually include different faunal areas, especially at the periphery.

Marked variations in endemicity may occur within a focus. An area may become rapidly hyperendemic as the numbers of vector *Leptotrombidium* and host *Rattus* or other theraphions (small mammals) greatly increase following the drastic modification of a uniform type of habitat, as when trees are felled for timber, or a garden is abandoned. It is still not adequately appreciated that places notorious as foci of scrub typhus can change over the period of a few years to the point where the infection is rare or absent in local chiggers and theraphions. This decrease in endemicity has been associated with the ecological succession of trombiculids and rats that can occur as the vegetative cover and the microhabitat change with the passage of time. Comparisons regarding endemicity should therefore be based on data collected in different areas simultaneously and not years apart, since the key feature is not the specific location, but rather the *contemporary* fauna of chiggers and hosts.

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In view of this time-factor and the fact that *R. tsutsugamushi* infection may exist in (or be absent from) an area despite its physiognomy, it is clear that one can no longer recommend aerial photography as a means of rapid detection of hyperendemic terrain.

Chigger-borne rickettsiosis is considered to be an evolutionarily youthful phenomenon as compared to infections like plague, and particularly, tick typhus. The group of *Leptotrombidium* vectors, their *Rattus*-hosts, and the secondary-type of vegetation with which they are associated, are all believed to be modern developments, geologically speaking, and the first two factors have presumably originated in S.E. Asia or the nearby islands. It is therefore to be expected that (1) both *Rattus* (*Rattus*) and the vector group of *Leptotrombidium* should be absent deep in unmodified areas of primary forest (except for penetration along water-courses and game trails, etc.); (2) in areas like New Guinea far from the epicenter of *Leptotrombidium*, there would be only a few species of *Leptotrombidium*; and (3) they and their *Rattus* (*Rattus*) hosts would be highly restricted to the forest edge in such remote regions. Recent data support these contentions. Since chiggers are the reservoirs of the infection in nature, as well as the vectors, introduction of a few infected individuals would probably soon seed a microfocus with the rickettsiosis through the mechanism of transovarian transmission of rickettsiae to the next generation. In this way, the delay caused by a build-up of a pool of infected hosts in order to maintain the infection is obviated.

In a fundamental way, chigger-borne rickettsiosis well fits the concept of a man-made disease. All of the known outbreaks have been the result of human modification of the environment, e.g., cutting of forest to build roads or camps or for agricultural settlements; abandonment of agricultural fields for military reasons; exposure of large bodies of susceptible individuals in infected foci; changing the course or level of rivers etc. Extensive and intensive timber operations have literally eliminated or drastically altered vast stretches of primary forest in Southeast Asia and the Australo-Asian archipelagoes and have created huge new foci of chigger-borne rickettsiosis as a result. If such activities were coupled with suitable preventive measures, or if the authorities would heed lessons learned with so much difficulty in the past, such outbreaks would not occur.

Murine typhus is another important rickettsial infection whose presence is often overlooked until cases unexpectedly occur. The disease has been reported on all continents and undoubtedly is far more common than records indicate. The main change in the concept of the ecology of this widespread infection is the realization of how little is actually known about the subject despite study in many parts of the world. It still is not clear as to how the rickettsiosis is actually acquired, and the literature is both confused and confusing, especially regarding serological tests that cannot be evaluated. It is generally accepted that infection is the result of contamination of the skin or mucous membrane with the infective feces of fleas, particularly *Xenopsylla cheopis*, or by contact with crushed fleas harboring *Rickettsia mooseri*, as shown in a critical review of the pertinent literature in preparation. Commensal rats (*Rattus*) are intimately associated with the ecology of murine typhus, and there is evidence to implicate, in varying degrees, lice, blood-sucking mites, chiggers or rats and perhaps ticks, as vectors. Contamination with urine of infected rats has also been suggested as a source, as has an aerosol of dust containing flea feces or dried arthropods, or secretions or excretions of infected murines.

Outbreaks have occurred where both rats and *X. cheopis* were supposed to have been rare or absent and there are other reasons for doubt as to whether this flea really is the main vector. Six genera and seven species of fleas have been found naturally infected, and most of these are rat fleas, the exceptions being the cat flea and the human flea, both of which may also feed on rats on occasion. Mammals that come in contact with commensal *Rattus rattus* or *R. norvegicus* may also become infected with *R. mooseri*, e.g. other *Rattus*, *Mus* (house mice) and even cats and opossums. There is virtually no evidence implicating feral, sylvan or campestral mammals in the cycles, but the limiting factors are not yet known. The foci seem to be indoors and apparently ultimately derived from association with *Rattus*. The infection may prove to be focally distributed within an endemic area. In North America it has been stated that the infection is essentially limited to the warmer parts of the U.S., but *Rattus* is distributed much further north than are cases, or infection in rats.

It is thus clear that there are many unresolved questions about the ecology of murine typhus, but the deep involvement of commensal *Rattus*, and perhaps *Mus* in the cycles of this infection automatically incriminates man as a potent factor in the incidence and distribution of this rickettsiosis. Rats and mice have accompanied man on his peregrinations over much of the globe, and the current crises over peridomestic and commensal murines in many of the most "advanced" parts of the world are especially deplorable because the entry and build-up of populations of rats in many

areas are recent, and indeed, contemporary events. Rat infestations are increasing in number and degree both in modern cities and in undeveloped and remote countries and are rapidly penetrating areas where they were unknown a few years ago. Control of rats and their ectoparasites are obviously essential for economic reasons as well as for sanitation and preventive medicine but few effective results are being achieved. While we may not be certain as to how murine typhus is transmitted, there is ample evidence that control of rats and their fleas can effect a marked decrease in the incident of this infection, viz a reduction of 96% in 6 years in the U.S. The current status of murine typhus as a problem should be re-evaluated in all known foci, and appropriate measures taken for its prevention and control.

Changes in the Epidemiology of Dengue and the Emergence of Dengue Hemorrhagic Fever

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ABSTRACT

Since the late 1950's epidemics of classical dengue fever have more and more frequently been accompanied by epidemics of an acute hemorrhagic disease, which has been defined as dengue hemorrhagic fever (DHF). In the vast majority of cases DHF has been associated with transmission by a single vector, *Aedes aegypti*, although other closely related vectors may play a role in the epidemics of classical dengue fever in the Eastern Hemisphere. The precise pathogenetic mechanism for DHF is still a matter of some debate, but the appearance and spread of the syndrome appears to many workers to involve human exposure to greatly increased populations of *Aedes aegypti*. This, in turn, is associated with rapid urbanization of tropical and subtropical populations; without, in many cases, the provision of adequate sanitary facilities.

The control of DHF epidemics in heavily populated areas, has largely involved the development of rapid methods for adult mosquito control, particularly ultra low volume insecticide application by ground and aerial methods. Complete evaluation of such methods has not as yet been possible, but they appear to be very promising.

The natural history of dengue virus has been investigated in Malaysia, and it now appears that dengue, like yellow fever, involves a jungle cycle and simian hosts. Man, living in or entering these habitats becomes infected with a relatively mild dengue fever, which may be all but inapparent, but which may be transported in viremic humans to villages or urban areas.

Introduction

The focus of the present review is on the effects of urbanization and changes in agricultural practices on the epidemiology of dengue. Agricultural practices have had relatively little effect on dengue, as compared with their effects on other arthropod-borne diseases such as malaria; although it is possible that some of the insecticide resistance in *Stegomyia* mosquitoes discussed below may be related to agricultural uses. The effects of urbanization have, however, been most dramatic. Gordon Smith (1975), citing Halstead (1970) discussed the possibility that the exceptionally dense populations of *Aedes aegypti* (L.) in cities of tropical Asia may have given rise to a new epidemic and fatal form of dengue known as dengue hemorrhagic fever (DHF). This syndrome has been described in detail by Halstead (1970) and others, and ranges from a moderate exacerbation of the usual hemorrhagic tendencies of dengue, through frank hemorrhage from the body openings, to shock and death.

Classical dengue fever has been the subject of an excellent review by Wisseman and Sweet (1961). With minor exceptions dengue had been until the late 1950's considered to be a debilitating disease of relatively short duration and not life-threatening. In endemic areas the disease, usually in the form of a relatively mild fever, attacked children for the most part, and might be relatively

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unnoticed. The major portion of the adult population might have positive serological responses. In such areas the introduction of non-immunes such as troops, laborers or migrants would usually be followed promptly by a clear cut and readily identifiable epidemic.

Theiler and Downs (1973) and Wisseman and Sweet (1961), however, point out the difficulties in commenting on early epidemics of dengue, since it is now known that dengue-like disease can be caused by a variety of arthropod-borne viruses, including chikungunya, sandfly fever and West Nile viruses. Furthermore, true dengue may exhibit a wide range of clinical symptoms ranging from a mild undifferentiated fever, through typical dengue with headache, severe joint pain and maculopapular rash or other minor haematologic manifestations.

It was a matter of more than slight surprise and alarm for public health authorities when Hammon and his associates first reported in a series of papers (Hammon et al. 1961) that the etiological agents of fatal disease outbreaks in children in Asia (Manila and Bangkok) were members of the dengue virus group. These consisted of the two serotypes described by Sabin (Dengue 1 and 2) during the Second World War and two new closely related agents (Dengue 3 and 4).

Urbanization

The effect of urbanization on mosquito-borne disease, particularly in the developing world, has been the subject of several recent reviews (Surtees 1971, Gratz 1973, Smith 1975). It is a matter of increasing concern, and not one likely to be solved in the near future.

In many tropical areas of the world the population is still growing rapidly, and many rural inhabitants are moving to cities at an accelerating rate (Gratz 1973). In many cases this has strained national resources to the point where many cities are ringed by slums constructed of tin and mud, and without adequate water or sewage facilities. While some progress has been reported many countries of the developing world are not particularly sympathetic to population control (Omran 1974).

It has long been apparent that increased urbanization of African and Asian cities has been accompanied by increases in populations of urban mosquitoes, particularly *Aedes aegypti* and *Culex quinquefasciatus* (=fatigans) Wiedemann. Surtees (1975) has noted that urbanization should ideally lead to a reduction in the number of naturally occurring breeding sites, through adequate sanitation and water control. However, the result in tropical areas of the underdeveloped world has often been just the opposite, often resulting in an increase in disease, and perhaps the emergence of new diseases such as DHF. In Asia there appears to have been a marked increase and spread of *Aedes aegypti*, often at the apparent expense of the native species *Aedes albopictus* (Skuse) and its close relatives. The latter point is, however, still open to some interpretation and question. *Aedes aegypti* entered Asia from Africa, presumably via sailing ships, at some time in the undefined past, but it was already present in numbers in coastal Asian cities by the time of the first systematic searches for possible yellow fever vectors in the early 20th Century. Such searches were apparently stimulated by the worry that the opening of the Panama Canal might open Asia to invasion by yellow fever. At that time, cities such as Bangkok and Singapore were quite small and somewhat rural in appearance. They have since undergone explosive growth, increasing several hundred percent in population and taking on a completely urbanized appearance.

The Genesis of Dengue Hemorrhagic Fever (DHF)

When DHF was first reported it was believed that its clinical manifestations might be due to a new virus, or to a particular strain or strains of dengue virus. Chikungunya virus, isolated in some of the episodes (Bangkok, Calcutta) appeared to be the cause of rather milder more typical "dengue" attacks. Attempts to prove that special strains of dengue virus were responsible for DHF have not succeeded and no really satisfactory laboratory model has been developed, except for some work by Halstead with monkeys. The most commonly accepted theory for the etiology of DHF, developed largely by Halstead (1970) and his associates, is that it is an immune response, perhaps due to the depletion of components of complement (WHO 1973), and that this results from infection of the individual by several strains of dengue virus in fairly rapid succession.

Since urbanization in Asia has led to vastly greater populations of *aegypti*, one might expect that the potential for DHF would be particularly great in such large concentrations of people and this

has been precisely the case. The disease appeared first in the large cities, and later in the more rural areas, but generally among significant concentrations of people.

Pant et al. (1973) compared the distribution of *Aedes aegypti* and *A. albopictus* with the distribution of DHF cases in portions of Thailand. DHF was first found in Thailand in Bangkok and subsequently appeared to spread along main arteries of commerce to smaller human concentrations. *Aedes aegypti* was found in all of the areas where DHF was found. *A. albopictus* was found in many areas but not abundantly in the larger cities. However, where *albopictus* alone was present DHF did not occur. Similar observations had been made by other workers (Scanlon 1965, Rudnick et al. 1967). It has been widely postulated that *Aedes aegypti* has been replacing *Ae. albopictus* since *aegypti* was first transported to Asia from Africa.

Through most of tropical Asia the *aegypti* model for DHF appears to be reflected in events in nature, but it is not universally accepted. In Singapore, K.L. Chan et al. (1971) found high populations of both *Aedes aegypti* and *A. albopictus* in areas of the Republic where cases occur, and dengue was isolated from both. Rudnick and Chan (1965) also isolated dengue virus from both species in Singapore, but only once from *albopictus*, while Chan and associates had more isolations from *albopictus* than *aegypti*. Furthermore, the latter workers felt that rather than *aegypti* replacing *albopictus* by competitive displacement, *aegypti* merely took advantage of what were in essence new, artificial and abundant breeding sites not exploited by *albopictus*. As the breeding sites spread *aegypti* would also, without necessarily replacing *albopictus*, which might continue to thrive if appropriate habitats were present (Y.C. Chan et al. 1967). These findings are quite similar to unpublished observations of the writer in Bangkok, and the findings of Gould et al. (1971) on Koh Samui Island in the Gulf of Thailand.

Whether *Aedes aegypti* or *A. albopictus* is the more important vector in a given area (and the weight of evidence overwhelmingly favors *aegypti*) the important question remains of whether or not multiple infection with different dengue serotypes is the triggering mechanism for DHF. The evidence from most of Asia favors this hypothesis. However, apparent DHF, some with shock and death, have been reported from the Pacific and the Caribbean in which primary attacks of dengue seem to have been involved. Some questions arise as to the precise definition of the DHF syndrome, and whether or not the cases seen elsewhere are precisely the same as those described from Southeast Asia.

At least another possible explanation has been offered for the DHF syndrome. During his research on jungle dengue Rudnick (1975) has demonstrated a very high level of antibody response in the "Orang Asli", aborigines of the Malayan forest, who live in areas essentially devoid of *Aedes aegypti*, but rich in *Aedes albopictus* and closely related *Stegomyia* species. He believes that the form of dengue seen in the *albopictus* jungle areas and the rural villages is the typical relatively mild dengue fever, and that DHF is seen only in the urbanized areas where *albopictus* is replaced by the more competitive *aegypti*. This concept of the vector acting selectively on the virus is an attractive one which has been discussed by many authors for various virus-vector combinations, but it has never been demonstrated adequately.

Given the hypothesis adopted by Halstead (1970) and others concerning the etiology of DHF it is readily apparent how urbanization has influenced the appearance and spread of the disease. That is:

1. The clinical manifestations depend upon infection of the host with two or more serotypes of dengue virus over a relatively short period of time.
2. The probability of this increases as the population of efficient vectors (*Aedes aegypti*) increases, and as the density of the human population increases.
3. The density of *Aedes aegypti* increases rapidly in Asian cities as the rural population moves to the urban areas, and as the urban populations themselves increase by reproduction. All too frequently this increase is much more rapid than the ability of the municipalities to provide piped drinking water to each dwelling.

If one accepts the alternative hypothesis put forward by Rudnick and others that classical dengue in Southeast Asia is a zoonosis, transmitted to man from monkeys by jungle mosquitoes, and from man to man in villages by *Aedes aegypti*, it is obvious that the more intense the urban transmission the greater the opportunity for the selection of the more virulent strains of dengue which the hypothesis holds to be the cause of DHF.

Reservoirs

Among the well studied arthropod-borne viruses, for which life cycles had been well worked out, it appeared until relatively recently that dengue was the only agent which was not essentially a zoonosis. From the time of the discovery of the sylvan cycle of yellow fever (YF) a number of investigators postulated the existence of a similar cycle in dengue. It remained for Rudnick (1974) and his associates of the Hooper Foundation, working in Malaysia, to demonstrate the involvement of wild simians in dengue in that area; first by serological demonstration of the infection of wild and sentinel monkeys, and later by the isolation of dengue-2 virus from the blood of a sentinel monkey exposed on a platform in the forest canopy. These results do not appear to have been duplicated elsewhere. Rudnick and others have postulated that dengue viruses may have originated in the forests of Southeast Asia and that they may be maintained there in a forest mosquito-monkey cycle, with occasional infection of forest dwelling humans (the orang asli of Malaya). In the latter connection it is interesting to note that Rudnick has reported the infection of these forest aborigines with all four types of dengue virus, based on serological evidence. There is at present apparently no evidence that non-human primates or other vertebrate reservoirs occur in other parts of the world. This would appear to confirm the suspicion of many workers that dengue viruses have their origin and center of distribution in Southeast Asia, with *Aedes albopictus* (*sensu latu*) as the natural vector.

Recent Epidemics

In the years since the WWII there had, until recently, been a relative recession of classical dengue fever, but more recently there have been a number of sharp outbreaks, some accompanied by DHF, or a similar syndrome. In the Caribbean epidemics of dengue occurred in 1963-64, 1968-69, 1971-72, and most recently in 1976-76 in Puerto Rico. In this latest epidemic three cases with symptoms suggestive of DHF have been encountered, but these appear to differ in some details from the DHF seen in Southeast Asia (Cline et al. 1976).

In the latter area dengue is endemic, and the syndrome known as DHF appeared first in Manila in 1959, followed by major outbreaks in Bangkok, Penang, Singapore and Kuala Lumpur. In 1973 over 34,000 cases of DHF and 613 deaths were reported to the WHO in 1973. The disease has now become firmly established in countries such as Thailand and appears each year in significant numbers. The peak year for Thailand appears to have been 1972.

Dengue hemorrhagic fever has also occurred in major epidemics in Indonesia and India, and in Burma in recent years. In the Pacific area there had been relatively little dengue since the major epidemics of the 1940's. During the past few years, however, increasing urbanization and air travel appear to have contributed to epidemics of dengue fever in French Polynesia, American Samoa, Fiji, Gilbert and Ellice Islands, New Caledonia, New Hebrides, Western Samoa and Papuan New Guinea (Chow 1974). *Aedes aegypti* was the vector most commonly found, and in several localities (Fiji, Naoru, etc.) cases of what appear to be DHF have appeared. In at least one instance, at Niue Island, DHF symptoms were detected in what appeared to be primary cases of dengue.

Despite the fact that Africa is the original home of *Aedes aegypti*, and the intensive urbanization there, and despite serological evidence of dengue infection in man, and a small number of dengue virus isolations in Nigeria, there do not appear to have been any large outbreaks of dengue fever in Africa in recent years, and no evidence of DHF. The reasons for this are unclear, but perhaps some virus interference phenomenon is involved, since a number of other group B arboviruses are active in Africa.

In South America, a dengue epidemic was recently reported in the Upper Magdalena River area (Groot 1976), probably of very large magnitude, but so far without DHF cases having been detected.

On a worldwide basis there appears to be some reason to believe that dengue cases, and dengue hemorrhagic fever cases, are spreading, although dengue has not reappeared in the temperate areas of North America, Europe or Japan as yet.

The Interruption of Epidemics

At present there is no vaccine available for dengue, and control must be based primarily on reduction of *Stegomyia* mosquito populations. In the major population centers of the affected portions of the world this essentially means control of *Aedes aegypti*, although it may be necessary to

control *Aedes albopictus* in Southeast Asia, and *Ae. scutellaris* (Walker), *polynesiensis* Marks and related species in the Pacific.

For long term control of *aegypti* the obvious need is for enforcement of proper sanitation, supplemented by larvicides. The present review, however, is concerned with the interruption of epidemics, and while larval control may play an important role in this, the obvious need is for the reduction of the adult populations of potentially infected mosquitoes as rapidly as possible. The World Health Organization teams in Bangkok, Jakarta and in the Pacific have published a number of excellent papers on the control of *Aedes aegypti* adults, particularly by the ULV method, both ground and aerial (Pant et al. 1971, 1973, 1974, Chow 1974).

Several reports have been issued recently on the interruption of dengue or DHF epidemics. Gould et al. (1971) used both larviciding and adulticiding on Koh Samui Island, with promising results in a small epidemic. Panthumachinda et al. (1974) applied the same techniques (abate larvicide and malathion ground ULV) in Chantaburi, Thailand and observed a 50 percent reduction in DHF cases. Pant et al. (1974) reported a sharp drop in hospitalized cases of DHF in Semarang, Indonesia following an aerial spraying with ULV malathion. The reduction began immediately following spraying and may be difficult to interpret. In Menado, Indonesia, Self et al. (1975) reported a sharp drop in cases some twelve days after ULV malathion spraying, which they felt corresponded to the incubation period of the disease. Cline et al. (1976) reported preliminary data on ULV malathion spraying from Puerto Rico which also suggest a considerable decline in *Aedes aegypti* populations and new cases of dengue.

In assessing all of these uses of apparent interruption of epidemics it is important to remember that in almost no case was it possible to have an adequate untreated check or control area.

In planning for the interruption of epidemics, as well as in routine control measures, one must also consider the troublesome question of the development of resistance. This has not as yet proved to be a serious problem with *Aedes albopictus*, but it has become of increasing concern with *Aedes aegypti*. WHO (1976) reports that in the Americas a protracted attempt to eradicate the species has resulted in almost universal resistance to the usually used organochlorine pesticides, as well as resistance to organophosphates in a number of areas. In Asia resistance to chlorinated hydrocarbons is widespread, and organophosphates resistance has been reported from Vietnam. Recently, resistance to bioresmethrin, a synthetic pyrethroid, has been reported in *Aedes aegypti* in Bangkok. If confirmed this would appear to dim the hopes somewhat for a class of pesticides which were counted upon to replace organochlorines or organophosphates where they became ineffective. There remain, in any given area of the world a number of pesticides for *A. aegypti* control, but the situation must be continuously evaluated.

As noted, *Aedes albopictus* is now resistant to organochlorines in several countries of Southeast Asia and the Western Pacific. It is also resistant to malathion in South Vietnam and fenitrothion in Madagascar (WHO 1976).

As new insecticides are substituted it is unfortunately true that the cost of operation continues to rise at a precipitous rate. Programs for *Aedes aegypti* control which might have been just barely manageable for some developing countries will become impossible if more and more expensive pesticides must be substituted. The possibilities for increased epidemic spread of dengue are obvious in this dilemma.

Ultimately, the control of dengue in the crowded cities of the tropical and subtropical areas must be based on environmental sanitation, as a continuous effort, rather than sporadic responses to epidemics. An outstanding approach to this has been made in Singapore (Chan et al. 1973) which involved a high degree of public health education, law enforcement and surveillance. The success of such a program thus depends to a large degree on cooperation of the public, and additional studies are needed on means to obtain such cooperation. An interesting study of this type was reported recently by Dobbins and Else (1975) in Malaysia, but much more work is needed by behavioral scientists to provide guidance for effective control methods.

Similar recommendations have been made by Gilett (1975) in an excellent analysis of the need for consideration of human activities, customs and cultural background in the planning of arthropod-borne disease control activities, including dengue control. He states that "... the rate of development should be geared to the means for waste disposal. Man, every-day man should be made aware of the dreadful price he himself pays for this development in the shape of sickness, death and general unproductivity." Whether such a logical appeal can really influence the pell mell development and urbanization of the tropical world remains to be seen.

The source reduction efforts in Singapore (Chan 1973) despite their considerable success in reducing premise indices also illustrated the need for supplemental chemical (larvicidal) control. Such chemical control may be quite expensive, particularly if a chemical such as abate is required. Even source reduction is too expensive for long periods of time, unless carried on by an informed and educated populace.

The Future Course of Dengue

It is difficult to judge what the future may hold in terms of dengue epidemics, and what future changes may occur in the natural history of the disease. This symposium has addressed itself to the effects of urbanization and agricultural practices on the environment and indirectly on the ecologies of the several diseases under discussion. As we have seen there is a considerable body of evidence that urbanization is a prime factor in the spread of endemic and epidemic dengue, and perhaps more importantly in the exacerbation of DHF.

Despite the worldwide attempts at population control, the populations of many countries continue to expand at a rate markedly greater than advances in their economics. This can only lead to further deterioration in sanitary facilities, with accompanying rises in *Aedes aegypti* populations. If the most commonly accepted hypothesis is correct and DHF has its genesis in exposure to multiple dengue infections over a relatively short time span one may well expect further extension of the syndrome, perhaps in the New World.

Coupled with this latter possibility is the introduction of additional strains of dengue into areas where only one or two strains may now occur, Bruce-Chwatt (1973) and others (Basio 1973, Highton and Van Sommeren 1970) have commented on the role of aircraft in transportation of adult mosquitoes. With vastly increased air traffic the possibility of transportation of dengue-infected *aegypti* over long distances must be considered, as well as the movement of humans in a viremic state, even though such a viremic period may be quite short. Bruce-Chwatt (1973) has pointed out the immense increase in the numbers of international air travelers, and the increased speed involved. He notes, "The speed of air travel is such that infected persons may arrive at their destination long before the end of the incubation period, and thus may spread the disease before the symptoms are apparent." Thus, dangers exist both of the transport of vectors to uninfested areas, and of disease organisms into receptive areas — i.e., those where suitable vector populations exist.

If the hypothesis of infection with several dengue types in the etiology of DHF is correct rather remote areas might thus fairly quickly find themselves changing from dengue to DHF in a fairly short period of time — requiring a high level of surveillance for hemorrhagic manifestations wherever dengue occurs.

One of the most interesting epidemiological questions concerning *Aedes aegypti*-borne disease is why yellow fever (YF) has not spread to Asia, despite the large (and growing) populations of *aegypti* in Asian cities and the large volume of travel from India, with perhaps less than perfect immunization status. Since Philip (1958) has demonstrated the susceptibility of Asian *Ae. aegypti* to YF virus, a number of workers including Max Theiler, have postulated that the high level of dengue antibodies in the human populations in Asia particularly in the port cities, has tended to interfere with YF transmission, even should the latter virus be introduced. Recently, Theiler and Anderson (1975) have demonstrated that prior infection with dengue virus in monkeys tends to lower the titer developed in later YF infection, perhaps enough to prevent infection in *Aedes aegypti*. Thus the presence of dengue in Asia, despite the threat of DHF, may protect against the incursion of the far deadlier yellow fever. However, Frederickson (1955) made retrospective observations in dengue and YF in the Americas which would appear to argue against this hypothesis — as do observations in Africa in the early part of the 20th Century.

There are a number of areas of developed countries, such as the Gulf Coast of the United States which appear to be in a receptive state for dengue. High levels of *aegypti* have been found in Houston by this investigator and his associates and Carmichael (1975) has reported from New Orleans that *aegypti* oviposited in all months of 1975, with a peak in May of up to 67 percent positive containers. This, despite serious efforts to again eradicate the mosquito. *Aedes aegypti* has again appeared at a number of points in Latin America where it had been eradicated, or had simply disappeared. It would thus appear that the situation may be ripe for a number of outbreaks of dengue similar to the epidemic reported from Colombia (Groot 1976). In New Orleans malathion and dibrom were effective against *aegypti* (Carmichael 1975) but given the large scale use of organophosphates for

agricultural purposes it is difficult to say how long such conditions will continue. Fortunately, *Aedes aegypti*, unlike rice field breeding *Anopheles* is relatively sheltered from selection by agricultural chemicals except in the rural fringes of the populations.

Overall, the most probable scenario for the immediate future involves additional and more widespread epidemics of dengue, and the extension of DHF to new areas. In reaching this conclusion the following elements have been considered:

1. The continuing growth of cities, particularly in the developing world.
2. The vast increase in air travel, and its increasing speed.
3. The continuing spread of insecticide resistance, the increased cost of insecticides and the decreased rate of development of new compounds.

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The Changing Pattern in Transmission of Bancroftian Filariasis

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ABSTRACT

In the first part, reasons are given for confining the discussion mainly to *Wuchereria*. It is also pointed out that transmission covers the whole field of epidemiology so only certain aspects more directly related to changes in transmission are discussed, namely: distribution of the disease and changing patterns created by its spread and its vectors, with emphasis on pullulation of *Culex fatigans* in undersanitated urban areas and insurgence into suburban and semirural areas. Control of the vectors and the growing opposition to the use of insecticides is mentioned plus the unexpected effect of larviciding on potential transmission. The importance of the new diagnostic techniques for revealing low density microfilaraemia and the infectability of such low densities for vectors is discussed. As always, taxonomic studies lag behind. There has been more support for such studies on the worms and these have yielded important results. It is pointed out that there is no International Reference Center for mosquitoes. The difficulties of comparing results from far and wide is largely the result of the lack of standardization, improvement is urgently required if changes in transmission are to be evaluated with any seriousness.

The filariases are considered to cover human infections with *Wuchereria*, *Brugia*, *Loa*, *Dipetalonema* and *Mansonella*. I propose to deal mainly with the periodic *Wuchereria* for several reasons. Firstly, it is the most important for man and our state of knowledge of the epidemiology and pathology of *Dipetalonema* and *Mansonella* is not very extensive. *Dipetalonema* is usually considered to be non-pathogenic or only mildly so over most of its distribution except Rhodesia (Clarke 1971) where it may be represented by another species. Secondly, our knowledge of the vectors of these two genera of filariae is on the whole poor. For example, what is presumably a single species of *Mansonella* occurs in vectors belonging to 2 different families of Diptera, namely, Simuliidae and Ceratopogonidae. Unless we are again dealing with two different species of parasite this seems unlikely.

Loiasis is now better understood largely due to the work of Duke and his collaborators at the Helminthiasis Research Unit, Kumba, Cameroon. The discovery of a sibling species, *Loa papionis* Treadgold, a parasite of the lower primates and its vectors is important as it offers scope for a laboratory model so sadly lacking in *Wuchereria*. Loiasis is, however, restricted to the African rain-forest, attacks small communities near the fringes and disappears with urbanization. The vectors are species of *Chrysops* (Tabanidae) and no dramatic changes in transmission are likely unless the parasite becomes adapted to savanna and grassland species of vectors. Dr. T.C. Orihel has shown that this is not so unlikely by the establishment of cyclical transmission in baboons and monkeys with a parasite from Africa related to *Loa loa* (Guyot) and an American vector *Chrysops atlanticus* Pechuman (WHO/MPD/75.5, p. 12, unpublished).

Apart from the work in Malaya (Edeson and Wilson 1964), the situation regarding *Brugia* is not clear. New and suspected vectors are coming along at a steady rate, new foci are being discovered, one or two old ones have disappeared and altogether it is difficult to detect any trends indicating changes in the pattern of transmission that is so obvious in periodic *Wuchereria*. The same could be said of subperiodic *Wuchereria* where it appears that each isolated group of islands has its own vector.

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The pattern of transmission of the filariases is continually being affected and changed for better or worse by a host of factors. Some of these are obvious, others not. Many of the latter are now being investigated and with the advent of renewed interest in these diseases we may expect some fruitful developments (WHO/MPD 75.5, unpublished). There will, of course, always remain some obscurities which are inherent in all biological systems but these should not interrupt progress towards control.

Transmission is not a single isolated and independent event and the vector is not a flying syringe loaded with disease. This is obvious but it bears repetition and reiteration as witness the very title of this symposium which implies that vectors bear, carry or transmit diseases. They do no such thing: they transmit pathogens. This is not merely quibbling or a question of semantics. I believe it is responsible for many mistakes in the past and even some at the present time when the whole emphasis is placed on attempts to get rid of the vectors, the so-called "carriers of disease," while the large number of factors involved in successful transmission are neglected. Some of these factors are only just coming to light as witness the recent discovery that the Fy Fy blood group genotype, found predominately in African and American blacks, is the *Plasmodium vivax* (Grassi and Feletti) resistance factor (Miller et al. 1976). How much more remains to be discovered? As Soulsby and Harvey (1972) have put it, "There has been little attempt at a multidisciplinary examination of the factors that determine the interaction between host, vector and parasite." Transmission is a dynamic system of which the vector is only a part and it covers the whole of epidemiology. To discuss this, I take it, is quite beyond the expectations of this group so I shall restrict myself to those aspects which appear to be more important and more relevant to the subject.

Events Causing or Likely to Cause Changes in Transmission

1. Distribution

This is not the place to detail the worldwide distribution of the filariases. Suffice it to know that they occur in one form or another in a wide tropical and subtropical belt between about 40° north to just under 40° south of the equator (Hawking, F. "The distribution of filariases throughout the world" Part I 1971, The Pacific Region, including New Guinea WHO/FIL/71.94: Part II, 1973, Asia: WHO/FIL/73.114, Part III 1974, Africa: WHO/FIL/74.124, unpublished). Here I will merely direct attention to those aspects which are germane to the particular argument. The most important of these are the discovery of new foci and the spread of the disease.

Evidence from many sources indicates that some filariases are spreading both inter- and intracountry. In both situations problems may arise with respect to new vectors, changed human ecology, changed climate and new conditions caused by population movement. Many of the recently discovered foci are in fact old ones which have been missed in the past or have not been looked for. There is, however, at least one instance of intercountry spread, namely, to Burma where filariasis was undoubtedly introduced. Prior to 1941 transmission was minimal or unknown (Tin Maung Maung and Botha de Meillon 1963, unpublished report to WHO) and local Burmese were not infected though infection was common among immigrants from India. The destruction by bombing, during the last world war, of the highly efficient existing sewage system and the failure to repair it plus the massive influx of wartime refugees gave rise to a concentration of susceptible hosts and a tremendous population of *Culex fatigans* Wiedemann (= *Culex quinquefasciatus* Say) estimated at about 44 million per square mile (Lindquist et al. 1967). By 1965, 4.2% of Burmese of all ages were found to be infected by ordinary blood slide examination (WHO Filariasis Research Unit, unpublished monthly report for January, 1965).

With regard to local or spread within a country there is evidence that this is a real threat in the Oriental and Subsaharan regions. In the former it may be mentioned that in India alone the population at risk has nearly doubled to 122 million since 1960 including both rural and urban areas (World Health Organization 1974, Raghavan 1957, and Gratz 1973.)

Many workers in Africa are of the opinion that filariasis is not only increasing in prevalence but also in distribution. Evidence of this comes from: West Africa and Madagascar: (Subra 1975). Seychelles: (Lambrecht 1971). East Africa: (White 1971).

That filariasis has disappeared from some areas is also known. Parts of the Mediterranean, Australia and Reunion are now free of periodic *bancrofti* and Ceylon of *Brugia*. Over 20 years of malaria control by indoor spraying, improvement in living standards and self protection have played a major role in Reunion (Brunhes 1975).

2. Vectors

The situation in the Oriental and Pacific regions is far from clear, and some complications are now arising in the Subsaharan. In the First Report of the WHO Expert Committee on Filariasis 1962 the list of vectors contains 5 species not mentioned in the Third Report 1974 and the latter now mentions no less than 29 species not noted in the 1962. Needless to say the taxonomic status of some of these species is in doubt so we may expect some changes. The vectors in some localities are as yet unknown so we may therefore expect some additions to the already formidable list.

It is generally agreed that apart from the important work done in Malaya (Edeson and Wilson 1964) much remains to be done in Asia and the Pacific. Some of the problems are already being investigated as witness the work on the mosquitoes of Tonga by the Medical Entomology Project, Smithsonian Institution and the Johns Hopkins University. There is no doubt that the results of these investigations will lead to changes in the pattern of transmission.

The best and most outstanding evidence of a changing pattern — apart from Rangoon already noted — comes from Subsaharan Africa, Madagascar and islands in the sea of Zanz. Briefly, the situation, until quite recently, was that in all West Africa and most of East Africa including the coastal islands (the situation in Central Africa is largely unknown), the vectors of periodic *Wuchereria bancrofti* were rural species of *Anopheles* whose control called for indoor spraying with insecticides. This pattern, however, soon began to change with the advent of a different class of vector with a different biology and ecology, namely, *Culex fatigans*. The rise and spread of this species was well documented by Mattingly (1962). Since then numerous authors both in East and West Africa have found evidence of this phenomenon in both urban and suburban localities (Hamon et al. 1967, Lambrecht 1971, White 1971, Subra 1975). Subra (see above) has drawn attention to the fact that in East Africa and islands *fatigans* is now not only an urban species but also becoming widespread in rural areas. He maintains that throughout this area *fatigans* is already transmitting *bancrofti*. Recently large numbers of *fatigans*, as much as a hundred or more per hut, have been found in some semirural areas of the Transvaal lowveld. In the early 1930's indoor spraying with pyrethrum in the same area produced none (unpublished personal observation). The threat of the spread of filariasis to this region from an infected neighboring country is a real one. This change has come about, as elsewhere, through urbanization or semiurbanization proceeding faster than sanitation and resistance to insecticides of *fatigans*.

In West Africa, so far, *fatigans* is said still to be restricted to the urban areas where it is apparently not transmitting *bancrofti*. Experimentally, however, it has been found to be receptive to the parasite and it is probably only a matter of time before filariasis becomes an urban disease. Subra (see above) who has investigated the epidemiology in West Africa and elsewhere for many years concludes: "La colonisation du milieu rural par *C. p. fatigans* évoquée à la fin de ce travail amène l'auteur à conclure que la transmission de la filariose par ce moustique n'est plus seulement un problème des zones urbaines, mais aussi de toutes les zones occupées par l'homme."

The changed situation that has developed and continues to develop still further in the Subsaharan region is mainly the consequence of economic pressures on the population causing a drift to suburban, urban and industrial areas. This unfortunately is not often or hardly ever accompanied by adequate facilities for waste disposal. The result is the accumulation of polluted waters in pit latrines, drains and other places and so creating the very conditions which cause *fatigans* to flourish. (Gratz, N. 1974, "Urbanization and filariasis" WHO/FIL/74.119, unpublished). The situation is tragic for the developing countries who, largely because of other priorities, have not the funds to undertake the necessary action for safe waste disposal which, after all, will provide the answer to the battle against *fatigans*. Another consequence of development in W. Africa has been the creation of storage dams, reservoirs and so on. This has led to the founding of a stable all season population of *Anopheles gambiae*, a very potent vector of *bancrofti*. Formerly this species was active largely during the rains and transmission was intermittent, now it persists throughout the year with dire clinical consequences. (Brengues, 1975).

The situation in Central and South America is largely unknown (WHO/MPD/75.5, unpublished). The vector is said to be *fatigans* and one may expect the same developments to take place here as elsewhere.

In the Orient, the situation is equally disturbing as has been recorded, among others, by Singh (1967) in Southeast Asia, by Dobrotworsky (1967) in the South Pacific and in Papua New Guinea by van den Assem and Bonne-Wepster (1964).

There is another aspect of *fatigans* biology that greatly enhances its vector potential thence the pattern of transmission especially where it is increasing in density. Here I refer to the discovery made in Rangoon (de Meillon et al. 1967) that large numbers of *fatigans* rest outdoors; that these mainly feed on man and that their *bancrofti* infective rate does not differ significantly from those caught resting indoors. This, of course, instantly changed the pattern of control which up to that time had been based on indoor insecticidal spraying (and had been singularly unsuccessful) and the pattern of transmission which was thought to take place indoors only. The same authors in Rangoon suggested that outside transmission might account for the higher infection rates in Indians, who being the poorest of the ethnic groups, were found to be among the only people who slept outdoors unprotected by house, screens, adulticides, bed nets and so on. In contrast, Europeans who head the economic list, and are best protected, have never been known to contract filariasis in Rangoon (Hairston and de Meillon 1968). The influence of human biology and ecology on transmission is, of course, well known and has been well documented in the Pacific (Jackowski and Otto 1955) and elsewhere (Dunn, F.L. 1974, "Human behavioural factors in the epidemiology and control of *Wuchereria* and *Brugia* infections." WHO/FIL/74.122, unpublished).

3. Control of the Vectors

There is ample evidence from Rangoon (Graham, J.E. et al. 1971, "Studies on the control of *Culex pipiens fatigans* Wiedemann" WHO/VBC/71.268, unpublished) and East Africa (World Health Organization 1974. 16-17) and from the Comores (Subra et al. 1973) that with larvicides the density of *fatigans* can be brought to a very low level. Unfortunately, epidemiological assessment of transmission has not kept up with the entomological achievements, a not unusual occurrence I may say in the sphere of the arthropathogen diseases. Little therefore can be said. However, there is one rather disturbing fact that has come out of the Rangoon experience and that is that larval control results in a rise in the proportion of surviving parous females after two years of larviciding and what is more, such a change in age structure of the vector population is reflected in increased transmission potential (J.E. Graham, et al. 1971, "Changes in the age structure of *Culex pipiens fatigans* Wiedemann populations in Rangoon, Burma after intensive larviciding" WHO/VBC/71.301, unpublished). If this turns out to be a common phenomenon associated with larval control then changes in transmission may be expected or at least must be looked for. The phenomenon has no ready explanation but serves once again to remind us that biological systems are complicated and that the results of interference in them by man cannot be anticipated or forecast with any accuracy.

Resistance to insecticides is a serious problem these days. Evidence for DDT resistance as far as *fatigans* is concerned comes from just about all parts of the world where tests have been made. Quite apart from resistance *per se* in *fatigans*, it appears to be accompanied by an increase in biotic potential resulting in an enormous increase in numbers of that species as reported both in India (Joseph et al. 1960) and in Africa (Smith and Bransby-Williams 1962).

Apart from resistance other objections to the use of persistent insecticides are gaining momentum resulting in increased interest in biological control. So far there are not enough data to draw any conclusions but it is quite probable that if and when applied unforeseen and unexpected consequences will result. One thing is certain and that is that the pattern of transmission will be affected.

One sure method of dealing with *fatigans* is the adequate disposal of wastes. Unfortunately the costs are high and prohibitive to most developing countries if we think in terms of modern sewage disposal in developed countries. However, much can be done to alleviate the situation among poorer rural communities where water supplies are limited. The work being done in Rhodesia is a fine example of this. A pamphlet kindly sent to me by Dr. V. de V. Clark of the Blair Research Laboratory, Salisbury, deals with 2 types, the "Watergate Unit" and the "Ventilated Dry Privy System." Both are in use and both are proving to be adequate to prevent *fatigans* breeding. ("Sanitation and Hygiene in Rural Areas" Blair Research Laboratory, Causeway, Rhodesia). Application of the principles of "bonifica integrale," so successfully applied in parts of Italy in the early 1930's, is still the safest and most effective way of dealing with many of the arthropathogen diseases. However, such a campaign has to be based on a sound knowledge of vector biology and human ecology so as to avoid the well intentioned but tragic consequences such as developed in Ceylon following the large-scale construction of pit-latrines (Abdulcader 1967).

4. *Microfilaraemia and Its Periodicity*

Microfilarial periodicity and subperiodicity which includes the nocturnal and diurnal forms of *W. bancrofti* are now well known. Each of these has the vector suited to its type of periodicity and this, of course, is very important because the more there is discovered about these periodicities and biting times of vectors the more will our understanding of transmission be affected.

In the first place it has recently been revealed that the old simple blood smear technique for detecting microfilariae is inadequate and that many more positives can be found by concentration techniques which had their origin in Knott's method for concentrating parasites in blood (Knott 1939). The older technique tended to miss the low densities and this has given rise to the importance of such positives and apparent negatives in transmission. The general opinion up to quite recently, and in spite of the work of Rosen (1955) and Wharton (1957), was that parasite control with diethylcarbamazine was the preferred method of control or even eradication (World Health Organization 1962:27). In some places complete or near complete success based on the old blood smear technique was claimed for parasite control. Since that time the picture has changed and the Third Report of the WHO Expert Committee on Filariasis 1974 has taken a more realistic point of view. In the light of further evidence recently produced (J. Bryan and B.A. Southgate 1973, "An investigation on the transmission potential of ultra low level *Wuchereria bancrofti* microfilaria carriers after diethylcarbamazine treatment" WHO/FIL/73.116, unpublished) it is now possible to disregard the old belief that the density of microfilariae had to reach a certain level before vectors became infected.

This relook at vector potential plus more refined methods of detecting microfilaraemia, mentioned earlier, are amongst the most important subjects likely to change our ideas of the pattern of transmission.

5. *Taxonomy*

Recent advances in parasite identification especially of the larval stages in the vector has thrown much light on our understanding of transmission. The outstanding example of this was revealed in Kenya where *Aedes pambaensis* Theobald was, by virtue of its high infection rate, thought to be an important vector of *W. bancrofti*. It subsequently turned out that all the larvae found in this mosquito were animal parasites belonging to no less than 6 different species (Nelson et al. 1962). Other instances of mistaken identity, no doubt, remain to be discovered. The importance of this aspect has been recognized for years and WHO has consistently supported research on identification of larvae in wild caught mosquitoes and for this purpose established the International Reference Center for Filarioidea in London.

The recent discovery of new species of filaria, namely, *Wuchereria lewisi* Schacher in Brazil and the Timor species, which as far as I know, has not yet been named, has added to the need for accurate identification of larvae in mosquitoes and this after all lies at the very base of the assessment of transmission and the incrimination of vectors. Accurate identification of vectors is equally important but there is no International Reference Centre for mosquitoes!

6. *Standardization of Techniques for Collecting Data*

Since the earliest days there has been a repeated cry for standardization but little has been achieved. The multidisciplinary nature of the subject involving, as it does, a whole series of biological and physical systems personed by an equally diverse group of investigators over a wide range of climate does not lend itself readily to standardization. That repeated efforts to achieve it should be made is undeniable because of the present day difficulties in interpreting results from various sources and making the necessary comparisons and evaluations. This is a long and diverse subject and it would be of no service to attempt an analysis here. It is sufficient to point out that the techniques employed and the subsequent interpretations have a strong influence on determining the pattern of transmission and the evaluation of the changes. Changes in transmission, if properly evaluated, will help tremendously in assessing failure or success in control or eradication. Even the commonest everyday words used in filarial epidemiology are variously interpreted and there is no glossary of terms as provided by WHO for Malaria Eradication. Such a glossary was prepared for the 1967 WHO Expert Committee Meeting on filariasis but it never saw the light of day.

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New World Leishmaniasis: A Review of the Epidemiological Changes in the Last Three Decades

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ABSTRACT

The epidemiologies of the 8 *Leishmanias* known to infect man in the Americas are defined briefly. Incidence figures and the distribution of human infection during the last 30 years are given where available, though it is emphasized that past documentation has frequently been inadequate. Leishmaniasis and its relationship to population movements and activities in agriculture, forestry, mining, construction and communications is described. Some outbreaks of the disease have occurred without apparent reason, and evidence for the possible influence of climate, animal disease and migration on the epidemiology is discussed. Established peri-domestic habits of some phlebotomines, and the apparent development of this type of behaviour in others is reviewed. The effectiveness of control measures against peri-domestic foci of leishmaniasis and their limited use, is contrasted with the impracticability of controlling silvatic forms of the disease. Although considerable advances have been made in understanding the complexity of leishmanial epidemiologies during the last decade, it is concluded that there is still a need for more comprehensive research in all New World countries where the disease remains a problem.

The distribution of leishmaniasis in the Americas extends from Mexico to Argentina with the strange exception of Chile and Uruguay (Pessoa 1972). It is known that there are at least 7 different *Leishmanias* which can cause cutaneous infections in man, and one which produces the visceral form. In a recent estimate Martins and Morales-Farias (1972) recorded 292 species of New World phlebotomines; 18 of these have been associated with the transmission of leishmaniasis, though only 11 can be considered as proven vectors (Lainson and Shaw 1973). Sandflies have been found from as far north as British Columbia and Alberta in Canada to La Plata in Argentina (Martins and Morales-Farias 1972).

How then have the 8 epidemiologies known to affect man changed in this vast area during the past 30 years? A review of the literature indicates that changes have taken place, though it is frequently necessary to interpret them with caution. In many countries observations lack continuity, which in part is linked to changing interest in the disease. Many forms of leishmaniasis are frequently confused with other diseases, due to inadequate or difficult diagnosis. This has resulted in records of apparent outbreaks of leishmaniasis in areas where it was previously unrecognized. For example, it was not until 1934 with the introduction of the viscerotome service for the diagnosis of yellow fever in Brazil, that visceral leishmaniasis was recognized as a problem in some areas (Pena 1934). Even today it is not unusual for our laboratory in Belém to be alerted to outbreaks of cutaneous leishmaniasis, which on closer investigation are frequently found to be tropical ulcer, yaws or even infected insect bites.

Notwithstanding such limitations, epidemiological changes have been observed and are most frequently related to increasing urbanization and exploitation of natural resources. Other outbreaks of leishmaniasis are possibly linked to climatic changes, which may alter the distribution of vectors,

reservoir hosts or man. Some of the better documented changes are the results of human attempts to eliminate the disease.

Due to their very different characteristics it is necessary to discuss the visceral and cutaneous forms of the disease separately. Short introductions defining the different epidemiologies are given, though it is clearly beyond the scope of the present paper to cite all the numerous original references on which these are based. For further details the reader is referred to the comprehensive reviews of Lainson and Shaw (1971, 1973) and Zuckerman and Lainson (in press).

American Visceral Leishmaniasis

Introduction

The causative organism of this disease is *Leishmania chagasi* Marques da Cunha & Chagas, which is transmitted by *Lutzomyia longipalpis* (Lutz & Neiva). Incrimination of this species as a vector is based on its identical distribution with that of kala-azar, and on records of naturally and experimentally infected flies. The dog is the principal reservoir host (Deane and Deane 1962, Torrealba et al. 1961), though the wild foxes *Lycalopex vetulus* and *Cerdocyon thous* have also been found infected (Deane and Deane 1962, Lainson et al. 1969). In most areas 70-80% of human cases are in children between the ages of 0-10 (Deane and Deane 1962, Torrealba 1964).

Distribution and Incidence

Twenty eight years ago New World visceral leishmaniasis had been reported in Brazil, Bolivia, Paraguay, Argentina, Venezuela and Columbia (Bustamante 1948). By 1964 cases had also been registered in Guatemala, El Salvador, Surinam, Ecuador and Mexico (Deane and Deane 1964). Subsequently infections have been diagnosed in Guadeloupe (W.I.) (Courmes et al. 1966) and Honduras (Nuernberger et al. 1975). It is highly probable however, that this apparently expanding distribution is a reflection of increasing interest and improved diagnosis, in countries where it has previously gone unnoticed. Thus, Deane and Deane (1962) pointed out that prior to 1952 only 33 human infections had been recorded in Brazil and visceral leishmaniasis was not considered to be a public health problem. In 1953, 46 cases were reported from Sobral in the north-eastern State of Ceará, Brazil (Aragão 1953), and this apparent outbreak resulted in the creation of a government agency to investigate and control the problem. Due to this stimulation of interest, the number of cases recorded in Brazilian medical journals rose dramatically to over 2,000 in the subsequent 8 years (Deane and Deane 1962). Similarly in Venezuela only 21 cases had been seen prior to 1960, though in 1961 Amaral et al. found a further 30, and by 1964 Torrealba had reached the conclusion that the true importance of kala-azar in Venezuela was still unknown. In the New World 3,200 cases of visceral leishmaniasis were recorded prior to 1964 (Deane and Deane 1964) of which 97.5% were from Brazil, and 1.5% from Venezuela.

In the last 12 years this pattern has remained similar though the number of cases has apparently decreased. Thus I was able to find records of a total of 571 cases since 1964, of which 501 (87.8%) were from Brazil, 50 (10.3%) from Venezuela and 11 (1.9%) from El Salvador, Guadeloupe, Honduras and Mexico. The decrease in numbers of cases is hopefully a sign that kala-azar is being brought under control. These figures may also, in part, reflect changing fashions in research, as Chagas disease and toxoplasmosis become more popular. Unfortunately the public health statistics available from the most highly endemic areas of Brazil (north-east) make no distinction between visceral and cutaneous leishmaniasis. However, recorded mortalities, which were presumably mainly visceral, show that 34 deaths occurred in that area between 1970-72 (Anon. 1971a, 1972, 1973). These figures plus reports of recent outbreaks in the States of Paraíba, Rio Grande do Norte and Bahia (Guedes et al. 1974, Fernandes et al. 1976, Chaddad et al. 1976), indicate that visceral leishmaniasis is still a matter for concern.

Epidemiological Change Through Control Measures

It would appear that intentional control measures against visceral leishmaniasis in the New World have, with the exception of Brazil, been limited to the detection and treatment of cases. Some

coincidental reduction in peri-domestic sandflies has however, resulted from anti-malaria and yellow fever campaigns. In the area of Pará State, Brazil where Chagas et al. (1937, 1938) reported *Lu.*¹ *longipalpis* in houses, we have on two occasions in the last 8 years been unable to find this species (Shaw, Fraiha and Ward, unpublished records). It is though that the disappearance of *Lu. longipalpis* in this case is a result of yearly anti-anopheline spraying. In Brazil, specific measures against kala-azar were carried out between 1953 and 1970 in the north-eastern States of Ceará and Bahia. These included the detection and treatment of human cases, the destruction of infected dogs and insecticidal spraying of houses and surrounding animal shelters. In a pilot project to determine the effects of DDT spraying Deane et al. (1955) selected 4 endemic areas, of which 2 were treated and 2 left as controls. A 3% aqueous solution of DDT was applied at about 2 gms/m². Sandflies were almost entirely eliminated from the houses and very few were observed four months later. Although an initial reduction in density was also recorded in the animal shelters, the population of flies had returned to normal within 3 months. By 1961 the anti-kala-azar campaign in Ceará had treated 2,096 human cases with antimonial drugs, poisoned 78,929 infected dogs with strychnine, and in the 14 sprayed areas reduced the incidence by 58.2% (Alencar 1961). In 14 untreated areas the number of cases had risen by 11.9% between 1953 and 1960. The reduction in the number of cases would possibly have been greater with more frequent applications of insecticide, particularly just before the onset of the rains, when *Lu. longipalpis* populations reach their peak (Alencar 1961). Between 1960 and 1962 it was noted that in all areas there was an increase in the percentage of urban cases (Alencar 1963). Thus in untreated areas, the percentage of urban cases rose from 9.1 to 20% and in treated sites from 6.7-21%. These changes were accounted for by the tendency of families to move to the towns and by improved transport between urban and rural areas.

Similarly between 1965 and 1969 control measures were taken in the endemic area of Jacobina, Bahia. In the treated area no human or canine cases were recorded in the last two years of the campaign (Sherlock and Almeida 1970). It was emphasized however, that natural inexplicable fluctuations in the incidence of the disease do occur, and that new efforts should be made to find other possible reservoir hosts and asymptomatic human cases.

Control campaigns in Brazil have been limited to endo-epidemic areas (Forattini 1973) though cases have been recorded throughout the north-east and eastern areas, and in the States of Goiás, Mato Grosso and Pará. In most areas, therefore, control is still unsatisfactorily dependent on the insecticidal spraying of the malaria campaign. For example, in 1974 the occurrence of 70 cases in Paraíba State was thought to be partly due to a cessation of anti-anopheline spraying 2 years earlier, and the subsequent reinfestation of houses by *Lu. longipalpis* (Guedes et al. 1974). As recently as this year (Fernandes et al. 1976), the occurrence of 17 cases in Rio Grande do Norte, Brazil, led investigators to emphasise the need for specific campaigns against kala-azar.

With the prolonged contact that peri-domestic sandflies have had with insecticides the possibility of future resistance should be borne in mind. Different species do apparently have varying degrees of susceptibility (Fedder and Alekseev 1961) and some isolated populations in Russia are said to be resistant to chlorinated insecticides. Populations of *Lu. longipalpis* from Minas Gerais, Brazil, have been exposed to the W.H.O. test and found to have LD₅₀'s of 0.55% for DDT and 0.24% for Dieldrin (Falcão 1963). It may be advisable however, to test flies from more highly endemic areas at frequent intervals.

Other Factors in Epidemiological Change.

Natural fluctuations in the incidence of visceral leishmaniasis in endemic areas and its appearances in apparently new foci, are probably related to animal and sandfly movements and population variations. Human migration and mobility also add to the changing pattern of the disease. Evidence for these changes in the New World is scarce and explanations are to some extent speculative.

One of the reasons suggested for the previously mentioned Paraíba outbreak was based on the movement of sick people. It was pointed out that pilgrims from endemic regions visit and remain in the area at certain times of the year, in search of faith cures from a "Miraculous Saint." The cessation

¹ The abbreviation *Lu.* is used throughout for *Lutzomyia* to avoid confusion with *L.* for *Leishmania*.

of malaria spraying and the domestic reinfestation with *Lu. longipalpis* could have opened the way for the introduction of kala-azar by the sick visitors to the area (Guedes et al. 1974).

In Brazil two large population movements have taken place recently which involved the endemic States of Ceará and Bahia. During the construction of the 1,600 km long Transamazônica highway and government controlled settlement of the area, approximately 22,000 people from the north-east and south have migrated there (Pinheiro et al. 1974). Although the majority were examined medically before resettlement, some may have been asymptomatic carriers like those recently recorded from Italy (Pampiglione et al. 1974a); others may have transported occult infections in their dogs. Some of the settlers were squatters and undoubtedly escaped any medical control. To date, however, no peri-domestic sandflies or human cases have been reported along the road. Similarly in Bahia the construction of a hydro-electric scheme at Sobradinho, has necessitated the transfer of approximately 10,000 families to other parts of the State. Population movements on this scale within and from endemic areas, may be reflected in future epidemiological changes. For example, Pampiglione et al. (1974a) emphasised the delicate immunological balance of asymptomatic carriers who may be provoked into typical cases when suffering from stress, famine, epidemic malaria or other infections.

The role of animal reservoirs in outbreaks of kala-azar is also not fully understood. There was a recent epidemic of 60 cases in Italy where only 4 had been recorded in the last 50 years. It was suggested that a drought in 1971 may have affected the behaviour of an unknown reservoir host, bringing it into closer contact with man and peri-domestic sandflies (Pampiglione et al. 1974). In discussing the apparently successful human control of kala-azar in Jacobina, Bahia, Brazil, Sherlock and Almeida (1970) pointed out that there was a concurrent reduction in cases from untreated areas. They noted that at the same time there was also an outbreak of rodent plague, which, with anti-plague measures, decimated the rodent population. Though no proof has been found that rodents are also reservoir hosts of kala-azar, this example does emphasise the need for further investigation and is a plausible explanation of how animal pathogens may alter the epidemiology of zoonoses.

The possible changing role of silvatic sandflies and those developing peri-domestic habits is worthy of consideration. It has also been suggested that other arthropods may be involved in the transmission of kala-azar. In Brazil, Venezuela, Guatemala and Mexico, *Lu. longipalpis* is the generally accepted peri-domestic vector (Deane and Deane 1964, Amaral et al. 1961, Leon and Figueroa 1959, Biagi et al. 1965a). Sherlock (1964) has however, indicated that canine cases have been found in Brazil in areas where *Lu. longipalpis* has not been caught, and has suggested the possible role of ticks in inter-canine transmission. In the Belém region of Pará, Brazil, foxes have been found infected (Lainson et al. 1969) though when they were used as bait in Disney traps only *Lu. flaviscutellata* (Mangabeira) was caught (Ward 1974).² It is thought that in this situation other sandflies may transmit among the wild reservoir hosts, which, when they come into contact with rural foci of *Lu. longipalpis*, may pass the disease on to the domestic cycle between dog and man (Lainson and Shaw 1971). *Lu. cortezzi* (Brethes) was found with *Lu. longipalpis* around houses in Minas Gerais, Brazil, where kala-azar had been reported (Martins et al. 1956). *Lu. evandroi* (Costa Lima and Antunes) and *Lu. oswaldoi* (Mangabeira) have been reported in houses (Deane 1956,³ Guedes et al. 1974), though the latter species has been observed feeding on lizards. In São Paulo State, Brazil, *Lu. intermedia* (Lutz and Neiva) and *Lu. whitmani* (Antunes and Coutinho) have been captured in large numbers in houses (Forattini 1960), though *Lu. longipalpis* is rare and cases of kala-azar unknown (Forattini et al. 1970).

In Sucre State, Venezuela, *Lu. evansi* (Nunez Tovar) was a suspected vector in the absence of *Lu. longipalpis* (Pifano and Romero 1964a), which was however, found there in later investigations (Henriquez et al. 1970). Similarly *Lu. atroclavata* (Knab) (= *Lu. gaudeloupensis*) has been suspected as a vector in Guadeloupe (Courmes et al. 1966) and was also recorded from hollow trees on Margarita Island, Venezuela, where one case of kala-azar was found in 1964 (Pifano and Romero 1964). Nine years later however, a further 3 cases occurred on Margarita, and *Lu. longipalpis* was found (Pifano and Morrell 1973).

²Ward, R.D. 1974. Studies on the adult and immature stages of some phlebotomid sandflies (Diptera: Phlebotomidae) in northern Brazil. Ph.D. Thesis Univ. Lond.

³Deane, L.M. 1956. Leishmaniose viscerale no Brasil: estudos sobre reservatórios e transmissores realizados no Estado do Ceará. Thesis, Fac. Med. Univ. S. Paulo, Rio de Janeiro: Ed S.N.E.S.

Lu. verrucarum (Townsend) and *Lu. peruensis* (Shannon) are highly domestic sandflies in parts of Peru, but there appears to be no records of the occurrence of cases of kala-azar. In Texas, USA, *Lu. diabolica* (Hall) has been found in houses (Lindquist 1936) though only imported cases of human and canine visceral leishmaniasis have been reported (Packchanian 1946, Ecker and Lubits 1947, Gleiser et al. 1957). Some workers have expressed their concern that such importation may be a public health hazard, it would however seem to be a relatively small one.

There are, therefore, sandflies which may be in the evolutionary process of becoming domesticated and others which are possibly vectors amongst wild animals. With further domestication or changing geographical distribution, it is not unreasonable to suspect that some could play a future role in the transmission of kala-azar to man.

New World Cutaneous Leishmaniasis

Introduction

The Parasites. — In the late 1940's New World cutaneous Leishmaniasis was thought by some to be caused only by *L. braziliensis* and *L. peruviana*. Others, however, did not recognize the Peruvian parasite and were of the opinion that in addition to *L. braziliensis*, the Old World parasite *L. tropica*, was present in the Americas (Bustamente 1948). In 1948 a third parasite, *L. enrietti*, was discovered in a laboratory guinea pig in the south of Brazil (Muniz and Medina 1948). This *Leishmania* normally only infects guinea pigs and its origin is still unknown. In the early 1950's attempts were made to differentiate between the clinical forms of leishmaniasis in man and 3 sub-species of *L. tropica* were named (Biagi 1953a, Floch 1954). Eight years later Pessoa (1961) named 5 sub-species of *L. braziliensis* as he was convinced that the New World parasites were not a result of importation of *L. tropica*. In 1962 Garnham gave *L. braziliensis mexicana* specific rank as *L. mexicana*, and more recently Lainson and Shaw (1972, 1973) classified the known parasites into the *mexicana* and *braziliensis* complexes, with 5 *Leishmanias* in each. Two other possibly new *Leishmanias* have also been discovered in wild animals from the Amazon region, though their significance and taxonomic position is still being studied (Lainson and Shaw 1973). Of the 12 known cutaneous leishmanias, 7 have been found to infect man. From this brief summary it is evident that only within the last 15 years has the existence of a variety of different leishmanial epidemiologies been recognised.

Distribution and Incidence. — Thirty years ago American cutaneous leishmaniasis was known to occur from Yucatan in the north to Argentina in the south, with the exception of Chile. The full distribution of foci of the disease within each country was, and is still unknown. As areas have been opened up, new foci have been identified, and in some cases destroyed along with the forest. This has been the case in São Paulo State, Brazil, where cutaneous leishmaniasis has been greatly reduced due to deforestation (Lacaz et al. 1972).

Records of the prevalence of the disease are believed to be inaccurate. This is mainly due to diagnostic problems, and because the infection is generally contracted by those working in remote regions, where communications and medical assistance are frequently inadequate. Lainson et al. (in press), noted that in the W.H.O. statistics report of 1968, only 71 cutaneous cases were recorded in the Amazon Region between 1940 and 1968. From the records of 2 clinics in that area however, they were informed of 633 cases registered between 1954 and 1968. A further 138 cases were examined in the Parasitology Department of the Instituto Evandro Chagas, Belém, Brazil, between 1968-1973. Even these figures are obviously only a small proportion of the true total. Intradermal tests in the Amazon region, have in fact indicated that between 32 and 58% of the rural population in some areas may have had leishmaniasis (Shaw, unpublished records). Similarly high percentages have also been recorded in Venezuela (Pifano 1962, Pons 1968).

To describe the changes in the epidemiology of New World cutaneous leishmaniasis it is necessary to consider separately each of the 7 parasites which affect man.

Chiclerós Ulcer or Bay Sore

Introduction. — The causative organism of this form of leishmaniasis is *L. mexicana mexicana* Biagi, and as its common and specific names indicate it has been particularly associated with chicle (chewing gum) collectors in Mexico. The disease is common throughout southern Mexico, Belize, Guatemala and may extend into Honduras (Lainson and Shaw 1972, Padilla and Lainez 1968). One

or a few cutaneous lesions are characteristic, and in up to 40% of cases these are situated on the ears (Martinez 1951). In a few unfortunate patients who have deficient immune responses, it may become diffuse and to date is incurable. The sandfly *Lu. olmeca* (Vargas and Diaz Najera) is considered to be the principal vector (Biagi et al. 1965), and small cricetid and heteromyid rodents are the reservoir hosts (Lainson and Strangways-Dixon 1964, Disney 1966).

Incidence. — Figures for chicleros ulcer, which was first observed in the Yucatan in 1912 (Seidelin 1912), have partly been complicated by the failure of patients to seek immediate medical advice. This can be attributed to the fact that most of them live in rural communities and can ill afford the time or money spent on seeking medical assistance. Torres Munoz (1953) in Mexico examined a woman whose ears had been infected for 12 years and a man who had the disease for 38 years. Between 1946 and 1955 only 66 cases were observed by the medical authorities in Belize (Garnham 1962). Lainson and Strangways-Dixon (1963) studied the disease there for 3 years and were of the opinion that the incidence is much higher than generally supposed. A skin test survey of 14 widely distributed communities in Belize, indicated that up to 9.2% of the population have at some time been infected (Chalmers et al. 1968). In Mexico an average of 34 cases per year were recorded between 1946 and 1955 (Garnham 1962), though previously in some areas as many as 17% of adult males have been found to be infected (Beltran and Bustamante 1942) and up to 71 new cases seen in one year. Between 1946 and 1948 the official annual incidence in Guatemala was 118 cases, though this figure dropped to 30 per annum in the subsequent 7 years (Garnham 1962). This change may reflect a decline in the chicle industry, due to destructive harvesting methods and the increasing use of vinyl resins and micro-crystalline waxes in the manufacture of chewing gum. I was unable to locate any official figures for the incidence of the disease in these countries since 1955. Their changing economies may have resulted in a decline in the number of cases, though some are still being reported (Novales 1974).

Chicleros are most frequently infected as they may spend up to 6 months of the year living in the forest. Men employed in mahogany, logwood and other timber cutting are also exposed to infection and cases are common in agricultural workers and road builders (Lainson and Strangways-Dixon 1963, Williams 1970). It is believed that chicleros are more commonly exposed to the disease as they spend the wet season in the forest, in contrast to mahogany cutters who are at work during the dry season, when the vector is less abundant (Williams 1965, Disney 1968). Biagi (1953) found that in a group of chicleros, 31% may become infected in their first season of work and a further 16% in the second year. In the Maya Indians who often work collecting chicle, 13-14% were found to have positive skin test reactions, compared with only 1.7-6.8% of Kekchi Indians who are traditionally farmers (Chalmers et al. 1968).

The number of men employed in forestry throughout these countries has varied due to many factors. In the Escarcega area of Mexico Biagi (1953)⁴ noted that the number of chicleros varied from year to year between 2,800 and 10,800. In 1959, Wright et al. estimated that there were 1,050 chicleros and 770 timber cutters in Belize. By 1970, Williams commented that the number of men employed in these professions was diminishing, as many were becoming agricultural workers. In Guatemala, a post-war slump in the chicle industry was followed by a recovery of exports in 1960 (Anon. 1971). Attempts to cultivate the chicle tree profitably in plantations have failed; it would seem therefore that the incidence of chicleros ulcer will largely depend in the future on whether or not chicle regains its popularity in the chewing gum, or other industries. The Yucatan, Belize and Guatemala are still, however, mainly covered in forest and most forms of economic development will continue to bring man into contact with the disease.

Climatic Influences on the Ecology. — Changes in the epidemiology of *L. m. mexicana* may be brought about by hurricanes (Lainson and Strangways-Dixon 1964, Williams et al. 1965, Lainson and Shaw 1968). Large tracts of forest in Belize were completely flattened in 1961 by a hurricane which destroyed the area where Lainson and Strangways-Dixon were trapping rodents. Some months after, much larger numbers of rodents were caught, which may have been due initially to a shortage of natural food. Later the tangled mass of fallen vegetation and dense secondary growth provided an ideal haven for an increasing rodent population and possibly more rodent leishmaniasis. Disney (1968) thought that the exceptionally deep leaf litter covering the forest floor after the hurricane,

⁴ Biagi, F.F. La leishmaniasis tegumentaria mexicana y algunos datos Medico-Estadisticos de Escarcega Camp. Thesis 119 pp. Mexico.

along with the very wet weather, would also have provided excellent conditions for the vector (*Lu. olmeca*). Given such circumstances it is easy to see how reservoir hosts and vectors may become adapted to secondary forest. *Lu. flaviscutellata*, which is closely related to *Lu. olmeca*, is abundant in some isolated pockets of secondary forest in the Belém area of northern Brazil (Ward 1974).²

Control. — Preventive measures against *L. m. mexicana* are to date impracticable. Insecticidal spraying of virgin forest, or destruction of reservoir hosts would clearly be a mammoth and uneconomical task. The use of repellants and screening is expensive to the generally poor forest labourer, and to date no safe or effective method of vaccination exists. The only certain way to eliminate the disease would be deforestation, but as H. Harold Scott once wrote this “would be like the Chinese idea of setting the house on fire to roast the pig.”

Swamp or Marsh Leishmaniasis

Introduction. — *L. mexicana amazonensis* Lainson and Shaw, the parasite responsible for this form of leishmaniasis, has been studied since 1963, though it was named only 4 years ago (Lainson and Shaw 1968, 1972). It has mainly been associated with marshy forests which are commonly situated at the bases of river terraces. The known distribution includes the Amazon Basin and Mato Grosso, Brazil, Trinidad and possibly southern Venezuela (Lainson and Shaw 1972, Tikasingh 1974, Pifano et al. 1973). The disease is uncommon in man and normally takes the form of a single or few lesions; like *L. m. mexicana* however, it is also responsible for the rare diffuse clinical form (Lainson and Shaw 1973). *Lu. flaviscutellata* (Mangabeira) is the vector (Lainson and Shaw 1968, Ward et al. 1973, Tikasingh 1975) and 8 species of forest rodents and 4 species of marsupials have been found naturally infected.

Incidence. — Of 108 parasitologically proven leishmanial patients, skin-tested in our Belém laboratory, Brazil, during the past 8 years only 10 (9.2%) were infected with *L. m. amazonensis* (Shaw and Lainson 1975). In Trinidad, 589 hospital admissions for the treatment of cutaneous leishmaniasis were listed during four years prior to 1931, though the identify of the causative parasites is unknown and the disease is a rarity there today (Tikasingh 1974). In the Amazon area, the low incidence in man was believed by Shaw et al. (1972) to be due to several factors. The marshy areas in which this zoonosis exists, constitute only a very small proportion of the estimated 7 million km² of land drained by the Amazon. These swampy forests have until recently been of little use for agriculture, though deforestation for buffalo rearing and irrigated rice cultivation are now more common. Some nuts and palm hearts are harvested from the marsh forests, though this is a daytime occupation and the vector is strictly nocturnal with a peak of activity between 21.00 and 03.00 hrs. (Lewis et al. 1970, Ward 1974).² In addition *Lu. flaviscutellata* is generally not anthropophilic and is only abundant during 4-5 months of the year.

Factors in Epidemiological Change. — It has been estimated that there are 25,000 km² of marshy forest in the Brazilian area of the Amazon Basin (Lima 1956). Up to 1970 in Pará State, only 20% of the rice crop was grown in swampy riverine areas, though yields there may be from 2-4 times greater than those on dryer land (Anon. 1970). More recently greater interest has been shown in this method of rice cultivation, and an American-financed company has deforested vast areas along the river Jari. The use of swampy land for agriculture is however, a relatively new concept in the area, and it will undoubtedly be many years before this development has any significant effect on the epidemiology of leishmaniasis.

Lu. flaviscutellata has also been found in dryer secondary growth forest, where average nightly catches in Disney traps have been as high as 108, only 28 less than the number caught in swamp forest (Ward 1974)². During the last year I have established 2 closed laboratory colonies of *Lu. flaviscutellata* in Belém, Brazil, from adults captured in secondary forest. One of these is now in its 8th generation and observations on the blood feeding habits, indicate that this species is more adaptable than previously thought. Surprisingly, in the initial generations the adults were 96% anthropophilic, though by the 6th generation 97.5% could be fed on hamsters. It is not unreasonable to suspect that the potential adaptability of *Lu. flaviscutellata* to different habitats and feeding behaviour, may in the future lead to changes in the epidemiology of *L. m. amazonensis*.

This disease has been reported in only a few patients from Venezuela, and is caused by *L. mexicana pifanoi* Medina & Romero. The clinical symptoms are similar to those observed in diffuse cases caused by *L. m. amazonensis*. Lainson and Shaw (1973) and Bray (1974) suspected that *L. m. pifanoi* and *L. m. amazonensis* may be identical. The isolation of parasites like *L. m. pifanoi* from *Lu. flaviscutellata* by Pifano et al. (1973) would appear to support this view.

Lack of information on the epidemiology of *L. m. pifanoi* makes any further discussion in the context of the present paper impossible.

Muco-cutaneous Leishmaniasis

This leishmaniasis which is caused by *L. braziliensis braziliensis* Vianna, is without doubt one of the most disfiguring forms of the disease. It has been recorded in Brazil, eastern Peru, Ecuador, Bolivia, Venezuela, Paraguay, Colombia, and is probably the parasite responsible for cases in Argentina (Villalonga 1963). The skin lesions may be single or a few and in some cases become very large. Three sandfly species have been proven to be vectors by inoculation of promastigotes into hamsters. They are *Lu. intermedia* (Lutz & Neiva) and *Lu. pessoai* (Coutinho & Barreto) in São Paulo State, Brazil, (Forattini et al. 1972) and *Psychodopygus wellcomei* Fraiha, Shaw & Lainson, in Pará State, Brazil (Lainson et al. 1973). Six other species of New World sandflies have been observed with promastigotes in their guts, but no isolations were made. *L. b. brasiliensis* has been isolated from four species of forest rodents in Brazil and a fifth is suspected. Isolations have also been made of a similar parasite from domestic rats in Brazil (Alencar et al. 1960, Lainson et al., in press).

Incidence. — Changes in the total incidence of New World muco-cutaneous leishmaniasis since 1946 are difficult to determine with certainty, as comprehensive records do not exist. *L. b. braziliensis* was defined only 4 years ago and therefore previous records undoubtedly include cases due to other parasites. In northern Brazil *L. b. braziliensis* has however, been the most common cause of cutaneous and/or muco-cutaneous leishmaniasis during the last eight years. Thus, of 108 parasitologically proven cases examined by Shaw and Lainson (1975), two thirds were caused by *L. b. braziliensis*. In the same area Silva (1973) recorded 378 cases between 1965 and 1970, and it is reasonable to assume that a similarly high proportion were caused by the same *Leishmania*. Barbosa et al. (1965) examined 150 patients in the State of Goiás, Central Brazil, between 1960 and 1965. It is in this region that the new capital Brasília was built, resulting in considerable immigration from surrounding areas and probably an increased number of cases. Due to past deforestation in the southern State of São Paulo, infections with *Leishmania* are becoming rarer; in contrast the opening up of new areas for farming in Parana and southern Mato Grosso States has resulted in an increase in the number of cases (Lacaz et al. 1972).

In one hospital alone in Bogota, Columbia, 519 cutaneous and 206 muco-cutaneous cases were registered in the 16 years following 1941; whilst for the whole country, there are records of nearly 2000 cases from 1948 to 1955 (Reyes 1959, Garnham 1962). Reports on the situation in Bolivia are a rarity. Twenty eight years ago, one case was described (Barrientos 1948) and Popper (1948) noted that "leishmaniasis is not seen in Chaco (S. Bolivia) but occurs in north-east Bolivia." To the best of my knowledge there were no further records for the following 26 years, until Walton et al. (1973) described four patients in which occult infections had taken from 11-24 years to develop characteristic naso-pharyngeal involvement. Two years ago, 113 cases were studied in the Coroico region (Desjeux et al. 1974) which clearly indicates the need for more information on the disease in Bolivia. Similarly, reports from Ecuador are rare and only a total of 67 cases were found (Carrera Cobos 1953, Rodriguez and Aviles Nugue 1953, Rodriguez 1969).

In Paraguay the incidence of 6,500 cases between the years 1942-1952 was greater than in Argentina where only 259 infections were seen during a similar period (Anon. 1968, Garnham 1962). The most recent report of Argentinian cases was in 1963 when infections in 23 children from Tucuman were recorded (Villalonga 1963). There appear to be no further Paraguayan cases registered. Peruvian incidence figures are complicated by the presence of *L. peruviana* Velez, the causative organism of uta. Garnham's (1962) statistics for Venezuela cited 4,264 cases between 1947 and 1955, scientific publications covering 1956-1961 gave a total of 502 cases (Anon. 1968) and those for

1962-1971 recorded 506 cases (Pifano 1962, Pifano et al. 1962, Pons 1968, Albornoz et al. 1969, Medina and Lizardo 1971).

Factors in Epidemiological Change. — Long term changes in the epidemiology of mucocutaneous leishmaniasis have been observed by Pifano (1960), during the establishment of farming communities in Venezuela. He defined three phases in the evolution of the disease as newly opened areas developed into established communities. In newly colonised areas there were many infections with simple skin lesions and a low percentage of the population reacted to the intra-dermal skin test. In a second phase many had active lesions whilst others bore scars of previous infection and between 5-10% suffered with naso-pharyngeal infections. Finally in old endemic areas a high proportion of the population bore scars, from 15-30% had mucocutaneous involvement and a high percentage were positive to the skin test. The pattern described by Pifano appears to have been the result of the immigration of mainly non-immune settlers. This, however, is not always the case, as was observed by Shaw (unpublished records) when he carried out a skin test survey during the construction and settlement of the Transamazônica highway, in Brazil. He found for example, that there was a much higher incidence of immunity in the bridge builders and early settlers who were mainly local people, than in the road builders, many of whom were from southern, non-endemic areas. There were however, very few cases in these people and the Government sponsored immigrants. Shaw felt that the absence of infection was possibly due to a lack of intimate man/forest contact, brought about by the use of mechanized techniques, and to the high incidence of immunity. He suggested that in time cases will become more frequent, particularly among the new, non-immune generations born in these locations.

In other areas high incidences have been observed during road construction and mineral exploration. Between 1970 and 1976, 52 cases of leishmaniasis caused by *L. b. braziliensis* were examined from a highly endemic area in the Serra dos Carajás, Pará, Brazil (Lainson and Shaw, unpublished records). In this area a large deposit of iron ore was discovered in 1967, and subsequently a mining feasibility project was mounted, covering 4000 km². Early in 1970 road construction began and an incidence of nearly one case per kilometer of road built was causing alarm to the camp doctor. At this stage members of our laboratory in Belém were requested to investigate the outbreak (Ward et al. 1973a, Lainson et al. 1973). Having established a road network in the first two years, the company then concentrated on establishing the depth and quality of the deposit. Less contact with the forest resulted in a 50% reduction in the number of cases from 35 between 1970-1971 to only 17 during 1972-1973. During 1974-1975 more topography teams were at work, which resulted in an increase to 25 infections. In the future, similarly high incidences can again be expected as a city is to be built in the area for those employed in ore extraction, and a 940 km railway is planned to transport the mineral to the coast. Other large iron and bauxite mining projects are underway elsewhere and no less than 30 hydroelectric schemes are planned in Brazil, which will undoubtedly result in the discovery of new foci of the disease.

The situation of South American Indians is an interesting one, since most groups have had a long history of intimate contact with the forest. Lainson et al. (1973) skin tested 116 Xikrin Indians who live only 60 kms from the Serra dos Carajás. None of the tribe showed any signs of active lesions or evidence of scars due to past infections. It was found however, that 83.9% of adult men, 38.8% of adult women, 14.3% of boys and 4.8% of girls had positive skin tests. These results are explicable by the fact that the men are constantly in much greater contact with the forest, whilst the women and children spend more time in their smoky camp sites. Similarly high levels of apparent immunity were found in 400 Indians living in the Xingu National Park, Brazil, and with the exception of the Waura tribe no clinical symptoms were observed (Aston and Thorley 1970). This tribe had been attacked for some years by the hostile Txikão Indians and had left their native forest and moved to the Xingu Park in 1962, where 12 out of 50 developed cutaneous lesions (Carneri et al. 1963). It would seem in this case that a move from a possibly non-endemic to an endemic area may have provoked the outbreak; or perhaps different *Leishmanias* were present in the two areas, and any acquired immunity from one gave no protection against the other.

The role of reservoir hosts of mucocutaneous leishmaniasis is still poorly understood, as few isolations have been made. Attempts to isolate the parasite from animals other than rodents have been unsuccessful, and there have been difficulties in culturing the parasite and infecting hamsters (Lainson and Shaw 1973). For example, in the highly endemic area of Serra dos Carajás, Brazil, although 75 rodents, 7 opossums, 9 monkeys and an anteater were examined, no infections due to *L. b. braziliensis* were detected (Lainson et al. 1973); *L. m. amazonensis* was, however, found.

An infected domestic rat was found by Alencar et al. (1960) in an area some distance from virgin forest. In a nearby house there were infected children who had apparently never ventured beyond the immediate surroundings. Lainson et al. (in press) have also isolated an *L. braziliensis*-like parasite from a domestic rat on the Transamazônica highway. These infections may be rarities but, perhaps in association with a peri-domestic vector could become more frequent and change the epidemiology of the disease. In Venezuela, dogs and donkeys have been found with lesions (Pons 1968) and in Ecuador, Carrera Cobos (1953) reported infections in dogs, cats, horses, agoutis and opossums. It is likely that in most of these cases infection was accidental, as in man.

In Aragua State, Venezuela, the population of a small fishing port and surrounding hamlets suddenly experienced an outbreak of leishmaniasis, in which 65 ♂ and 88 ♀ were infected between January 1966 and February 1968. Of the patients, 61.4% were children under 15 years old. No deforestation or road building was occurring in the region and it was hypothesized that an unknown reservoir host had invaded the area (Albornoz et al. 1969). The prevalence in women and children, plus the fact that house fumigation appears to have reduced the incidence for some months, suggests that peri-domestic transmission was occurring. During 1961-1965, in an area east of Belo Horizonte, Minas Gerais, Brazil, a range of 10-15 cases per year were observed. In the first 6 months of 1966, however, 27 cases appeared and Furtado et al. (1966) also emphasised that no connection with man's activities in the forest could be found.

There is little doubt that there are other vectors of muco-cutaneous leishmaniasis yet to be recognized. For example, *P. wellcomei*, the vector in the Serra dos Carajás, Pará, Brazil, has to date been found only there, though infections are common throughout the State. *Lu. intermedia* and *Lu. pessoai* were also incriminated as vectors in Brazil, but no definite isolations of *L. b. braziliensis* have been made from sandflies in other countries. The fact that 6 other sandfly species have been observed with promastigotes also clearly emphasises the need for more attempts to isolate and identify these parasites.

It is well known that many *Leishmanias* will develop in a variety of sandfly species (Lainson and Shaw 1973). In addition, experimental transmissions have been achieved using parasites foreign to the vector. Coelho and Falcão (1962) transmitted *L. m. mexicana*, with *Lu. longipalpis* and *Lu. renei* (Martins, Falcão and Da Silva), a species not found in Mexico. These transmissions indicate that in some cases there is no vector/parasite specificity, which means that new epidemiological situations may arise when host or vector distributions change.

Lainson et al. (1973) thought that the apparently normal daytime biting behaviour of *P. wellcomei* was an important factor in its role as a vector. *P. carrerai* (Barretto) has also been observed to be diurnal by members of our staff working along the Transamazônica highway. Reports of daytime biting sandflies have however, mostly been linked to exceptional climatic circumstances, such as increased rainfall, cloud cover or humidity changes. Short and long term meteorological alterations are well recognized phenomena and may be the cause of some apparently inexplicable changes in the epidemiology of leishmaniasis.

The infections in children from Ceará and the outbreak in a Venezuelan fishing village already cited (Alencar et al. 1960, Albornoz et al. 1969) are suggestive of domiciliary transmission. Twenty nine years ago Nery Guimarães & Bustamante (1954) studied a scattered rural population in Rio de Janeiro and found that 39 out of 306 people had leishmaniasis. They captured 132 *Lu. intermedia*, one of the known vectors, from a dozen houses. In 1948 the malaria service started regular DDT applications and by 1953 only one person out of 296 was suffering from leishmaniasis. No sandflies were found in houses at this time, though only 20 metres away *Lu. intermedia* was readily captured. Recently Forattini et al. (1973, 1976) also suspected domiciliary transmission by *Lu. intermedia* in the south coastal region of São Paulo. Peri-domestic infections may have occurred in Rio de Janeiro, Brazil, during 1974, when 8 out of 14 cases seen were children (Menzes et al. 1974). As discussed in relation to kala-azar, there is evidence that some sandflies are developing domestic or peri-domestic habits which could result in significant epidemiological changes.

Control. — The problems of prophylaxis against what is predominantly a silvatic disease, are the same as those discussed earlier for chicleros ulcer.

"Pian-bois" or Bush-Yaws

Introduction. — This disease is caused by *L. braziliensis guyanensis* Floch, and is found in the Guianas and also in Amapá, Roraima, Pará and Amazonas in northern Brazil. The skin lesions are

frequently multiple due to metastatic spread along the lymphatics. A sandfly identical to that identified as *Lu. anduzei* (Rozeboom) by Floch and Abonnenc (1944) has recently been incriminated as a vector in Monte Dourado, Pará, northern Brazil (Lainson et al., in press). Other sandflies from this area and *Lu. anduzei* from Surinam have also been found with promastigotes in their guts, though the identity of the parasites is unknown (Lainson, Shaw and Ward, unpublished records, Wijers and Linger 1966). No reservoir hosts have been found.

As recently as 5 years ago Garnham (1971) commented that "complete descriptions of the epidemiology and even the clinical features" of "pian bois," "have still not been published." The disease has however, been known for a long time, and was for example, first reported in Surinam in 1911 (Flu 1911). It was observed in convicts engaged in construction work in French Guyana during 1937-1938 (Floch and Abonnenc 1952), and in bush negroes and soldiers in Surinam (Bruijning 1957, Wijers and Linger 1966). Forattini et al. (1959) studied an outbreak which affected the workers of a manganese mining company in Amapá, Brazil.

Incidence. — The most comprehensive figures for the disease are those of Floch and Sureau (1952) and Floch (1953, 1957) who diagnosed 235 cases in French Guyana between 1935 and 1955. Only four cases have been studied in Guiana during the last 30 years, (Emslie 1962, Talbot and Hawking 1964) and although Wijers and Linger (1966) state that leishmaniasis may be contracted in all parts of Surinam, no figures appear to be available. In Amapá, Brazil, Forattini et al. (1959) observed 66 cases in only a few months of 1958-1959, and in Pará, Brazil, 30 cases from Monte Dourado have been diagnosed by Lainson and Shaw (unpublished records).

Despite the lack of information on the total number of cases, it should be emphasised that there is a very high chance of becoming infected in some foci. Thus, in recent investigations in the Monte Dourado area, 3 out of 7 of our laboratory team acquired the disease. Three other members became infected at the same time, though the identification of their parasites was complicated by the fact that they had been engaged in concurrent studies in another area (Lainson and Shaw, unpublished records).

Factors in Epidemiological Change. — In Monte Dourado a vast forestry programme is taking place, which involves as many as 1,500 men per year, employed in deforestation. It is intended to cut down and re-plant 2000 km², and 40% of this task has already been completed, in addition to the construction of 4,400 kms of road. There has been a high incidence of infection in the area and this will presumably continue until deforestation ceases. Re-forestation has been with pines and an African soft wood tree (*Gmelina*), and it remains to be seen if the reservoir hosts and vectors of "pian bois" will adapt to this new environment. This possibility seems remote in view of the dramatic ecological changes that have taken place.

Control. — In French Guyana, Floch (1957a) recommended spraying with DDT, BHC, or dieldrin in a radius of 250 meters around forest work areas, as an inexpensive measure against sandflies. He found that this treatment was effective for 1.5 months during the rainy season. Floch's experiments may well have been inexpensive for such a short duration, but this method of control would clearly be impracticable in large forestry development.

Panamanian Leishmaniasis

Introduction. — The causative organism of this form of leishmaniasis is *L. b. panamensis* Lainson & Shaw, which has been found in Panama, and possibly extends northwards into Central America and south into Columbia. Lesions are usually single, though may also become multiple due to metastatic spread. In rare cases the upper respiratory passages may be affected (Jaffe 1961), though the possibility that such infections are caused by *L. b. braziliensis* has been suggested. The Gorgas Memorial Laboratory team have incriminated *Lu. trapidoi* (Fairchild and Hertig) *Lu. ylephiletor* (Fairchild and Hertig), *Lu. gomezi* (Nitzulescu) and *P. panamensis* (Shannon) as vectors by the inoculation of promastigotes into hamsters. In Costa Rica, Zeledon and Alfaro (1973) isolated a *Leishmania* from *Lu. ylephiletor*, which appears to belong to the *L. braziliensis* group, and may prove to be *L. b. panamensis*. Three procyonid species and two species each, of rodents, primates and sloths, have been found infected naturally. It is not certain however, that all were definitely *L. b. panamensis* infections.

Incidence. — Before 1948 only 26 cases of leishmaniasis are on record in Panama, and in that year 12 more were reported, 6 of which were American soldiers (Snow et al. 1948). Five years later Calero and Johnson (1953) observed 25 patients, 23 of whom were farmers engaged in clearing forest

or planting and harvesting. These authors concluded that the disease was commoner in Panama than had previously been supposed. In 1968, Walton et al. (1968) also pointed out that the disease had, until that time, been considered of little significance to U.S. forces in the Canal Zone. For example, although many troops were stationed in Panama during the Second World War, only 4 cases were recorded. Between 1953 and 1965 however, 0-17 cases per year were registered in US soldiers and there was some evidence of peaks of incidence every 5 years. The high risk of infection run by soldiers on jungle manoeuvres was demonstrated in 1974, when 10 cases were seen in men who had only spent 10 days in contact with the forest (Kern and Pederson 1974). Similarly high incidences were observed by members of the Gorgas Research Institute in the Quebrada Bonita area, where 47 out of 82 (57.3%) settlers became infected in only 4 months (Wright 1970).

Approximately 60% of the population of Panama are engaged in some form of agriculture. Recently, Herrer and Christensen (1976a) have defined 3 patterns for the epidemiology of leishmaniasis in such rural communities. In the new settlement of Loma de Mercurio, 14 out of 33 (42.4%) apparently non-immune people, became infected within 1-14 months of exposure. The infections were in all age groups and both sexes, and no further cases were seen following the end of deforestation (Herrer and Christensen 1976). In the non-endemic area of Bayano however, infections were found in only 9 out of 161 (5.6%) of the population; 8 of these were men, who it was believed, had acquired the disease in forests far from the settlement (Herrer et al. 1976). A third situation was studied in the long established community of El Aguacate where 4 out of 5 (80%) cases were children. Of the adults, 59 out of 115 (51.3%) had scars from previous leishmanial infections. Part of the original forest in this area had been preserved, and this was presumably where each new non-immune generation became infected.

Factors in Epidemiological Change. — The reservoir hosts of Panamanian leishmaniasis belong to more diverse groups of animals than those of other epidemiologies described. Recently Herrer and Christensen (1976b) have also suggested that dogs may serve as incidental reservoir hosts, or as a liaison of infection between the forest and human settlements. They examined 333 dogs during 1968-1973 and found lesions in 11 (3.3%). Seven were hunting dogs, which presumably became infected when in the forest with their owners. Of 19 dogs examined with apparently normal skin, none were found to be infected. They pointed out that the reservoir hosts were driven away, following the destruction of jungle, yet in Quebrada Bonita where leishmaniasis no longer exists, sandflies can still be captured. From the clinical effects in dogs and the low percentage infected, it would seem more likely that dogs are in fact accidental hosts, as is man. Dogs and man could serve as a source of infection in such areas, but the chances of sandfly infections are much less than with natural reservoir hosts, where the parasites may be distributed throughout apparently normal skin.

Precipitin tests on the blood-meals of Panamanian sandflies have shown significant differences in feeding patterns for the same species, from one area to another (Tesh et al. 1972). These differences and seasonal variations in feeding behaviour were thought to be a reflection of the fauna available in each locality. The changing patterns of behaviour probably contribute to the marked focality of leishmaniasis, and are a potential for adaptation to the altered ecology of areas where man is active.

Control. — The impracticability of large scale adult sandfly control in forests has already been discussed for other areas. In Panama the scattered breeding sites of some vectors on the forest floor also means that insecticidal control of the immature stages is not feasible (Rutledge and Ellenwood 1975). As elsewhere, no effective vaccine exists and the only means of control is still the detection and treatment of cases.

Peruvian Leishmaniasis or Uta

Introduction. — *L. peruviana* the causative organism of uta is limited in distribution to the western Peruvian Andes; the skin lesions are single or a few, and generally heal without treatment. The association between uta and sandflies was suspected as long ago as 1764 by Cosme Beuno (Herrer and Christensen 1975). The probable vectors *Lu. verrucarum* (Townsend) and *Lu. peruensis* (Shannon) have, however, only been incriminated on the basis of their co-incidental distribution with that of the disease (Herrer 1951a). Dogs are the reservoir hosts, with infection rates as high as 56% (Herrer 1956), and generally, no lesions are apparent. The disease is contracted by people in, or around houses located in non-forested areas between 900-3000 m above sea level (Herrer 1957).

Incidence. — Herrer (1951) studied the incidence of uta in the rural areas of Huarochiri province, between 1943 and 1949. Infections were equally prevalent in males and females, but in highly endemic areas lesions were most common in children, with up to 90% infected or scarred. A single infection generally resulted in immunity, but in 2 cases re-infections were seen in people who had moved from one region to another. During the six year study, numbers of cases per year ranged from 8-48.

Control. — Between 1945 and 1947 Hertig and Fairchild (1948) carried out sandfly control tests with DDT. Houses and surrounding stone walls were sprayed with a 5% solution in kerosene, and sandfly populations were markedly reduced for 12-19 months. In two construction camps, sandfly control was followed by a virtual cessation of new cases of uta. Herrer (1956) reported that in the Canchacalla Valley there had been a reduction in the incidence of canine infection due to the use of insecticides by householders. Thus, the infection rate in dogs had dropped from 56.2% in 1945 to 14.7% in 1956. It was pointed out that no government or private spraying scheme had been carried out there, and that insecticide resistance could possibly arise as a result of uncontrolled private spraying.

I was unable to locate any further information on the disease in Peru for the period 1956-1976.

Conclusions

Within the limits of time and space in a paper of this nature, I have attempted to outline the ways in which the epidemiology of New World leishmaniasis has changed in the last 3 decades. The result can be compared to a jigsaw in which many of the pieces are missing, either because they do not exist or cannot be easily found. A principal factor in this incomplete picture is that it is only during the last decade that there has been a growing awareness of the many epidemiologies that exist. Even in places where the disease has been and is being studied, numerous questions remain unanswered, whilst in some countries investigations have been sporadic or almost non-existent. Many of the conclusions on past and probable future changes are therefore based on circumstantial evidence. There is a need for improved diagnosis and documentation of the disease throughout much of the New World. More widespread study by multi-disciplinary groups would also undoubtedly result in a greater understanding of the epidemiology of leishmaniasis, and the ways in which it is changing.

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Recent Changes in the Epidemiology of Malaria

Relating to Human Ecology

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ABSTRACT

The major factors of human ecology which influence or are likely to influence the spread of malaria are the growth of cities and towns (urbanization), transport and population movements, agricultural and engineering developments (irrigation and building of dams), changes in customs and habits and the introduction of a vector species into an unexploited habitat. Recent examples of changes in the epidemiology of malaria which are related to these factors are described. Prospects for the future control of malaria are briefly discussed.

Changes in malaria transmission related to spraying practices which have produced insecticide resistance, refractory behavior of a mosquito vector towards the insecticide and emergence of unsuspected or secondary vector species not controlled by practices directed towards the primary vector are considered beyond the scope of this review. The problem of drug-resistance is likewise an extremely important one which has been recently reviewed by others.

The accepted patterns for the transmission of malaria are changing in many areas of the world. Mosquitoes which were formerly considered to be vectors can no longer be found in certain regions or cannot be recognized in view of new concepts on the identification of species groups. In this context, *Anopheles gambiae* Giles is now known to consist of 6 species, 4 of which are referred to as *gambiae* species A, B, C and D; each of which has a distinct ecology. Cities or even nations which thought they had malaria well under control find themselves in the midst of epidemics of this disease. The promise which DDT and other persistent pesticides held forth have largely disappeared. Physicians and health authorities now find it difficult to treat cases of falciparum malaria in Asia and portions of the New World tropics due to the presence of drug-resistant parasite strains.

The purpose of this review is to re-emphasize that the epidemiology of human malaria is in a constant state of change which is closely related to the alteration of the natural environment by man. With the marked increase in human population over the past few decades, and increasing exploitation of a variety of habitats for the growth of urban centers and development of agricultural resources, it is not unexpected that such changes have occurred and will occur at a rapidly increasing pace.

It is not within the scope of this review to discuss these problems and changes in any depth, but it is hoped that the presentation of some recent problems in malariology will stimulate new interest in understanding and appreciating an old disease.

Attempts have been made by specialists to categorize these recent changes. The most useful classification has been made by Smith (1975) who recognizes 4 broad groups of factors which

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² This paper is dedicated to the memory of Professor Alfred E. Emerson.

influence or are likely to influence patterns of disease. These factors are often interrelated as this review points out, but they can be divided into: (1) the growth of towns and cities (urbanization), (2) transport and population movements, (3) agricultural and engineering developments (irrigation and building of dams), and (4) changes in customs and habits. To these might be added a 5th factor, the introduction of a vector species to an unexploited habitat.

Urbanization

Two recent examples will be cited to document the increase of malaria in large tropical cities; the first involves Karachi in Pakistan and the second involves Kinshasa in the Republic of Zaire.

Since 1941, Karachi has experienced considerable population growth due to immigration and natural growth. From a population of 387,000 in 1941, the metropolis grew to an estimated 3.8 million in 1968. The climate of Karachi is hot with minimal rainfall (less than 2.5 cm of rain had fallen during the first 8 mo of 1968) and the city is surrounded by semi-desert. Under these conditions, a rapid increase in malaria occurred from 1966 to the middle of 1968 when it was estimated that 10-20% of the population or 400,000-800,000 people had malaria infections (Carmichael 1972).

The vector was identified as *An. stephensi* Liston on the basis of epidemiological investigations which found sporozoite rates as high as 1.2% (Communicable Disease Center 1968). Anopheline larvae were found breeding throughout the city in surface water such as pools from leaks in the piped public water system, in household water storage containers and in effluents from sewage treatment plants. This water all originated from water piped into the city, sometimes as far away as 100 miles from the city.

This epidemic was clearly attributed to problems in the management of waste water which were beyond the control of municipal agencies at the time. Typical of this was that sewage effluent was discharged into adjoining dry river beds where *An. stephensi* breeding was abundant. Recommendations for control were made by a U.S. team of public health investigators which were primarily predicated upon source reduction procedures.

During the quarter of a century between 1948 and 1975, Kinshasa (formerly Leopoldville) has experienced a similar population growth. In 1948, the population was 126,000 and by 1975, it had increased 10-fold to 1.3 million. Prior to independence in 1960, malaria was well under control in this city where an active control program was in progress and waste water conducted away in well-constructed drains. Most new cases of malaria were attributed to introductions from the surrounding countryside where crops were grown for the city markets and movement of infected citizens along the Zaire (Congo) River.

In the absence of epidemiological data from Kinshasa in the post-independence period, aside from reports of medical officials that malaria was becoming more prevalent, a field study was conducted in Kinshasa during 1973 (R.A. Ward, C.L. Diggs, J.C. Burke and W.A. Reid, unpublished data). Children were observed with falciparum infections at an outpatient clinic of a hospital and visits made to their homes to determine possible sources of infection. In virtually all cases, *An. gambiae* (probably species A), was found breeding anywhere from a few to several hundred meters from a patient's home. Larvae occurred in all types of water, with the exception of fast-flowing ditches. Especially impressive was the observation that *An. gambiae* larvae were extremely abundant in highly polluted water containing household wastes. It was estimated that at the end of the rainy season in July 1973, the malaria infection rate approached 25% in the more recently developed areas of the city which lacked sanitary waste or storm water disposal facilities. Since *An. gambiae* larval breeding appeared to be so restricted to man-made habitats, it appeared reasonable that control could be readily initiated.

The process of urbanization may at times produce such unfavorable conditions, that malaria may disappear with minimal control activities. This was apparently a major factor in the disappearance of malaria from Great Britain in the early portion of the 20th century. In the Netherlands, the sharp reduction of malaria incidence since 1947 and disappearance by 1958, it attributed to a decline in the population of *An. atroparvus* van Thiel in the province of North Holland and the northeast Polder as a result of a marked decrease in the number of pig sties and stables where the females can feed and rest. Associated with insecticidal treatment, breeding places were found to be increasingly polluted with anionic detergents which are toxic to anopheline larvae at a concentration of 2 ppm (Seventer 1969).

Agricultural and Engineering Developments

Agricultural practices are known to have a profound influence upon the epidemiology of malaria. A review of the overall problem of the effects of irrigation on mosquito populations and mosquito-borne diseases in man was made by Surtees (1970). In virtually all instances where land is developed in the tropics from forests, or even plains which are subject to irrigation, serious malaria problems develop within a few years unless careful advance planning has occurred.

The increased significance of *An. balabacensis* Baisas as an important vector of malaria in Southeast Asia appears directly related to the destruction of tropical evergreen forests in the forested foothills of countries such as Thailand. When land is cleared for crops such as tapioca, an interface is usually left between freshly cleared land and the higher vegetated hills which are unsuitable for agriculture. This provides an ideal breeding and resting site for *An. balabacensis* which increases in numbers under such conditions. Its marked preference for human blood meals; its feeding behavior indoors and preference to rest outdoors in vegetation after a meal; its high level of susceptibility to infection with falciparum malaria and its great longevity make this species one of the most efficient malaria vectors known. Control of malaria under such conditions is extremely difficult, especially when drug-resistant strains of falciparum malaria are associated with this vector (Scanlon and Sandhinand 1965). Retrospective studies in some of the above areas of Thailand indicate that as the land becomes more intensely cultivated, and the hilltop remnants of forest are removed for firewood, the breeding sites of some of the larval *An. balabacensis* are removed with a resulting reduction in the adult population. Some larval breeding can still occur as it is a fairly adaptable species whose larvae can develop in small ground depressions or larger bodies of standing water such as rain-filled pits dug for the mining of sapphires.

The construction of great dams to form large reservoir lakes in Africa has had an influence on the incidences of diseases transmitted by aquatic molluscs and insects with aquatic larvae. Akosombo Lake was formed by the construction of a dam on the Black Volta in Ghana from 1964-1968. Its formation resulted in much increased production of the vector species *An. gambiae*, *An. funestus* Giles and *An. hargreavesi* Evans (Deschiens 1972). Similar problems have been predicted along the shores of Lake Nasser which was formed by the high dam at Aswan on the Nile. This entire problem is carefully analyzed by Stanley and Alpers (1975) in a recent book, "Man-made Lakes and Human Health".

Fortunately, through careful management, the construction of dams may also have a positive effect by decreasing the incidence of malaria vectors. Along the upper course of the Rio Parana in Brazil, extensive flooding occurred until various dams on the tributaries of the Parana and the main river were completed in 1968 and regulated the flow. After this period, marked decreases in abundance of *An. darlingi* Root and *An. albitarsis* Lynch Arribalzaga were noted once the dams controlled the floods (Consolim and Galvão 1973).

The Kunduz Valley of northern Afghanistan affords an excellent example of a complete change in malaria epidemiology in a desert-steppe habitat. Approximately 15 years ago, prior to the introduction of irrigation in the Kunduz Valley, *An. superpictus* Grassi was considered to be the most important vector species in this region. Its larvae lived in the only source of suitable water; small seepages of fairly clean water at the base of small hills. A number of other anopheline species were present but were considered to be of little or no significance in malaria transmission. Following the initiation of irrigation, large-scale agricultural schemes were developed for the valley with the subsequent planting of rice, cotton and melons as the main crops. Associated with this was an increase in both the human and cattle population. *Anopheles superpictus* disappeared from the Kunduz Valley as the natural breeding sites became contaminated from the activity of cattle and men. New larval habitats were created by the standing water in rice fields, overflow from irrigation ditches and polluted seepages. These provided ideal breeding conditions for *An. pulcherrimus* Theobald early in the malaria transmission season and for *An. hyrcanus* (Pallas) near the end of the transmission season. The incidence of vivax malaria rose from 5 to 25% in some villages over a period of 3 years as a consequence of these vectorial changes. At the present time, malaria control is difficult because *An. hyrcanus* is resistant to DDT and *An. pulcherrimus*, although susceptible, avoids surfaces treated with DDT. Transmission is further facilitated by the habits of the local inhabitants. During the melon-harvesting season, the men sleep in the fields to prevent theft of the crop and during the hot summer months, most of the villagers sleep outdoors in courtyards which are in close proximity to cattle sheds which serve as a further attractant for mosquitoes. Consequently, no protective measures are taken by the village inhabitants against mosquitoes (Buck et al. 1972).

Transport and Population Movements

Increases in malaria related to these factors are more difficult to analyze due to the length of time that is required for changes of this type to become evident and the fact that entomologists only become aware of these situations *de post facto*, with the obvious exception of malaria related to armed conflict.

The highlands region of New Guinea affords an excellent example of a rapidly changing pattern of malaria epidemiology. The inhabitants, who for the most part live in small villages or hamlets along valleys or on the tops of mountain ridges at an elevation of 1,300 to 2,500 m, had little contact with civilization until the 1930's or for some not until the 1950's. Most of this early contact was through administrative officials, mission workers and gold miners. The traditional routes for the entry of malaria into the relatively malaria-free highlands were through war parties, often cannibalistic, and trade journeys down into the hot, humid malarious areas of the Markham and Ramu valleys. Other cases of malaria were acquired during visits to the rich alluvial plains along the south bank of the Ramu River while cultivating gardens. Females usually exhibited higher infection rates than males as they traditionally devoted more time to gardening than males.

With the pacification of the highlands region and greater influence of missionaries in the post World War II period, the region rapidly became exposed to malaria through a variety of routes. These included the building of access roads and the creation of new labor markets. Numerous infection reservoirs were introduced by coastal workers who came from malarious lowland areas. By far the greatest source of new malaria cases came from highland laborers who worked on coastal rubber, coconut and cocoa plantations for relatively long periods of time before returning home. With the improvement of roads, a much greater interchange of people occurred. As an example, before a road from the Markham Valley was improved in 1968, the average number of vehicles passing through into the highlands was 15 daily; after improvement, 87 daily. Parasitological surveys made in 1965 indicated that 3.1% of passengers in the vehicles entering the highlands had positive malaria smears. Thus it is easy to determine the mechanism of rapid dissemination of malaria into this region.

The earthmoving associated with building houses and roads has created an abundance of new breeding sites for *Anopheles* species. In addition, the vehicles may also have served as a source of infected mosquitoes.

Early mosquito surveys (1945-50) indicated that *An. farauti* Lavarán was the most abundant vector species in the highlands of New Guinea. Although larvae were common around some of the towns, adults were relatively rare and the conditions of "anophelism sans malaria" prevailed in many areas. Malariometric data is scarce from the early period, but a survey in the Wahgi Valley during 1934-35 found 3.3% of children with palpable spleens. Surveys made in 1964, preparatory to initiation of a malaria control program revealed that both *An. punctulatus* Dönitz and *farauti* were present in houses, the former species in greater abundance. Larvae of both species were plentiful and there was a significant increase in the prevalence of adults as compared with earlier surveys. There was a corresponding increase in malaria in the Wahgi Valley in 1956 with as high as 78% of the blood films positive for malaria during an epidemic.

Since 1966, when an extensive program of residual spraying was initiated and a mass chemotherapy program developed, the average parasite incidence rate dropped from 13.8% to 0.3% by 1969. A small residual amount persisted due to the uninterrupted flow of traffic through the infected Markham Valley (Radford et al. 1976).

Mosquitoes are regularly imported into the Termez area of Uzbekistan, U.S.S.R. by river transport on the Amudarya between various Soviet and Afghanistan ports. *Anopheles pulcherrimus* Theobald, an important malaria vector of northern Afghanistan, is collected with high frequency from all types of vessels. This species is found in greatest numbers aboard during July and August when transmission is at a maximum level. Iadhieva and Abdullaev (1975) believe that foci of malaria are introduced annually into Termez by this mechanism.

During the past year, evidence was presented that *An. barbirostris* Van der Wulp, an Oriental vector, became established on the island of Guam (Ward et al. 1976). This species was probably introduced via cargo vessels or aircraft refueling on Guam en route from southeast Asia to the United States.

Changes in Customs and Habits

There are numerous instances where the acquisition of malaria is closely associated with special conditions of making a livelihood which have been altered due to economic or political considerations. Several recent examples of malaria transmission related to social conditions are described below.

A detailed analysis of the epidemiology of malaria in Trinidad in the 25 years from 1940-1964 indicates that cultural patterns of land use, migration and settlement and changes in mosquito abatement practices are all important variables for an understanding of the malaria picture in Trinidad (Fonaroff 1968). The subtle relationships between the association of *An. bellator* (Dyar and Knab), its bromeliad plant hosts, cacao growing with the associated lowland Bocare tree (*Erythrina glauca*) and the behavior of the East Indian cacao farmers all create the most complex pattern of malaria epidemiology known. This is probably one of the best studied examples of man-made malaria and serves to emphasize the malariological problems associated with artificial or cultivated tropical forests (Downs and Pittendrigh 1949).

During the period between 1947 and 1970, there was a significant reduction in the numbers of adult *An. atroparvus* Van Thiel found in animal sheds in southern Moravia, Czechoslovakia. Minar and Rosicky (1975) state that this is due to the fact that the large sheds which were erected for cattle or pig sties during collectivization proved to be less favorable resting sites than the smaller shelters which existed prior to the formation of collectives.

In West Malaysia and Singapore, the fruit of the durian is extremely popular. In order to prevent theft of the fruit, plantation owners stay up at night to collect the ripe fruits as soon as they fall. This has resulted in an increase in the incidence of falciparum malaria among people living and working in Kuala Lumpur, who are bitten by infected anophelines in their plantations at night from June to September (Ponnampalam 1975).

Introduction of Vector Species into New Habitats

The accidental introduction of a malaria vector into a new environment where it can survive is often the key factor in a change in the epidemiology of malaria. The situation in Brazil in which *An. gambiae* from Africa became established, its role in malaria transmission during the 1940's and its subsequent eradication has been well documented (Soper and Wilson 1943). A retrospective review of the malaria epidemic which occurred on the island of Barbados from 1927-1929 serves to further document this point.

Prior to 1927, there was no evidence that the principal malaria vector of the Caribbean area, *An. albimanus* Wiedemann, existed on Barbados, or if it did, it was not present on the leeward side of the island. During the spring of 1927, the normal dry season did not occur and small surface bodies of water persisted for many months. Anopheline breeding suddenly occurred in abundance along the western and southwestern coastal region during the spring and early summer. By the time *An. albimanus* was identified, more than 300 cases of malaria had been reported during October 1927. Medical records indicated that malaria had been regularly introduced into the island since 1920 by returning migrant male workers. Since no new transmission to other family members occurred until 1927, it was surmised that a vector was not present earlier. Fonaroff (1966) believes that a successful introduction of *An. albimanus* happened as a consequence of the abnormally favorable environment available in the spring of 1927. This introduction was most likely through the agency of coastal-plying vessels rather than wind dispersal due to the island's easterly location in respect to the other Antilles and the prevailing wind direction of the northeast trade winds.

Prospects for the Future

From the developments of the recent past, it can be assumed that malaria will continue to be a serious disease in the future. The increase in urbanization and development of land for agriculture and other purposes appear to present the most potential problems for the future. Other authors have stressed the role of intercontinental flight in transporting agents of infection and their arthropod hosts as an area for future concern, but this seems to be less important for malaria than for arbovirus diseases such as yellow fever and the dengue fevers.

In a literature search which was made during the preparation of this paper, little indication was found that many tropical cities could manage the vector-disease problems which have been proliferating at a rapid rate. Generally, those metropolitan regions which showed the highest rates of growth during the past 25 years have the most public health problems. A number of these situations (i.e., filariasis in Rangoon, malaria in Karachi and Kinshasa) have emerged due to the inability of the municipalities and their adjacent suburbs to handle the problem of sewage and industrial wastes or excessive rainfall. The creation of numerous small bodies of water, rich in organic matter, provides an ideal breeding site for a number of mosquito species (i.e., *Aedes aegypti* (L.), *Culex quinquefasciatus* Say (= *C. fatigans* Wiedemann), *C. tritaeniorhynchus* Giles, *Anopheles gambiae* and *An. stephensi*) and the ready availability of human hosts in high densities permits the rapid development of large mosquito populations. Consequently, it is not unexpected that epidemics of disease can occur over a very short period of time.

The solution of future problems of urban malaria appears to be one of proper urban planning. Entomologists and public health authorities should participate in the early stages of development. Whenever economically feasible, storm drains and sewers should be installed in areas where construction will occur. This is a far more practical procedure than to attempt to rebuild these systems 20 years after a new area of a city has developed while simultaneously carrying out a costly vector control program.

In contrast to the urban situation, there now appears to be a greater awareness in conducting large-scale agricultural and water management projects in respect to health problems than has occurred in the past. Examples of such advance planning are as follows:

- (1) Bayano River Project, Republic of Panama. — Ecological studies are being conducted on a large hydroelectric river impoundment in Panama by the Gorgas Memorial Laboratory. Special emphasis is being placed upon the impact of this project on arbovirus disease transmission cycles and the ecology of anopheline mosquitoes. These studies started prior to the initiation of the project in 1976 and will continue as a large lake is being formed. (P. Galindo, personal communication).
- (2) Atlantic Pacific Interoceanic Canal Study Commission. — Medical ecology studies were conducted from 1966-1968 by the U.S. Army Medical Department on potential canal routes in Panama and northern Colombia to identify actual and potential disease problems which might be encountered during the construction of a new Atlantic-Pacific canal (B.F. Eldridge et al. 1973).
- (3) Medical Research Council Project, Kisumu, Kenya. — A long term study on the effects of irrigation on local public health was started in 1970, several years in advance of irrigation. The advisors will devise and put into effect measures which will control the spread of disease once the risks have been assessed. Control measures will be monitored to prevent deleterious effects (Simpson 1975).

It is apparently easier to marshal the necessary resources and personnel (politicians, economists, engineers and scientists) to consider the consequences of these larger developmental projects due to the tremendous economic impact that successful development will have upon one or more nations.

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Anthropogenous Influence on the Existence of Natural Foci of Diseases

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ABSTRACT

The anthropogenization of environment, where seven principal stages may be distinguished, has been in progress during this century. The process of synanthropization of many epidemiologically important species has been lately in full development. Changing patterns in relationship in the system biotope-pathoergont-vector-vertebrate host showed, on the basis of our experiences from Central Europe, new epidemiological significance of the development prognoses of some natural focus diseases or diseases caused by arthropods. These phenomena should be taken into consideration in preparing surveillance programs and anti-epidemic measures.

During the thousand years' evolution specific biocenoses, communities of animals and plants have been created, achieving a certain balance in their spatial and biotic structure. The appearance of man as a biological species and particularly his influence relating to the rise of human society constitutes a milestone in further evolution of nature. Vigorous human activities have become manifest by still greater interference with original conditions. The initial man's activity as a hunter signified a minimal disturbance in the existing population numbers of some animal species which served as his food. Subsequent pasturing and agriculture, accompanied by deforestation and cultivation of vast areas represented a far more essential disturbance. In the first stage only local disturbance in the landscape was involved but later complete liquidation of parts of some biocenoses and their substitution by culturocenoses took place. These were the first beginnings of anthropogenous influence on the landscape, a still more advancing anthropogenization of environment. Its last stage is the present industrial exploitation of natural resources, construction of housing estates and communications systems and factory aggregations. From the aspect of landscape cultivation by man, from the viewpoint of anthropogenization of environment, we may consequently distinguish 7 principal stages (Rosický and Hejný 1959, Rosický 1975):

(1) The natural landscape. This stage includes original landscapes untouched by man's activities, characterized by typical phytocenoses and zoocenoses. It is extremely rare in European conditions but is still common in uninhabited regions such as tropical forests, deserts, semideserts, Siberian tiaga.

(2) The slightly cultivated landscape. The original, natural, usually zonal arrangement of the biogeocenoses is broken up by elements of cultivation, chiefly pastures, fields and meadows. The border line between the natural part of the region and areas altered by man is not yet completely defined phytocenologically.

(3) The moderately cultivated landscape. Natural biogeocenoses are scattered by cultivation measures into very irregularly distributed systems of natural, partly cultivated and cultivated parts of landscape. They are characterized by typical mosaic distribution of the different components of the landscape. The typical feature is the marked breaking up of coherent biogeocenoses. Phytocenoses in this stage are sharply defined.

(4) The highly cultivated landscape. Natural biogeocenoses have been in most cases replaced by cultivated or partly cultivated biogeocenoses. Natural units are confined to extremely limited but biocenologically very diverse enclaves. The main feature at this stage is the presence of only isolated groups of forest biogeocenoses.

(5) The completely cultivated landscape. Culturocenoses and substitute cenoses completely predominate in this type of landscape. Original biogeocenoses are either completely scattered or reduced to such negligible proportions that they can no longer give refuge to the original vegetation components.

(6) The devastated landscape. The natural biogeocenoses are completely destroyed by human activities in animal husbandry, natural resources exploitation or industry.

(7) The inhabited landscape. The natural biogeocenoses are very limited till completely absent due to the construction of human habitations, settlements, villages and towns during the progress in urbanization.

Human interference during cultivation of landscape is extensive, but it may be stated that lately the last 3 mentioned stages are particularly in progress.

After Pavlovsky's theory of natural focality of diseases (1939, 1964) the causative agent of a disease, its reservoirs and vectors, are members of certain biogeocenoses, in which the historically evolved circulation of pathoergont¹ takes place. Anthropogenous changes in a biogeocenosis also involve changes in spatial and biotic structure of natural foci; the primary autochthonous foci gradually get transformed into anthropourgic ones, predominant in the cultivated landscape. In the process of landscape cultivation distinct changes took place both in reservoirs and in vectors. The changed environment subjected some vertebrate species to unfavourable conditions, their numbers gradually decreased until they either disappeared completely or transferred to more suitable biotopes. To other species, on the other hand, the cultivated landscape offered optimal conditions for their existence. They were mainly vertebrates living in field culturocenoses where their numbers rapidly increased and often the hitherto range of their distribution became expanded. High numbers of some species, primarily of ungulates, have been also intentionally maintained by man for breeding and sport purposes. Similar tendencies in the decrease of population numbers until their complete disappearance, transfer to new biotopes may be also observed in vectors.

Anthropogenous influence consequently resulted in the disturbance of original ecosystems, changes of biocenoses, changes of living conditions and hereby of circulation routes of causative agents. New ecosystems have risen whose structure and topology entirely depend on human activities. In anthropourgic foci composition of biocenoses, behaviour of various components of the focus — the vertebrate hosts and vectors — intensively changed and necessarily also had an impact on causative agents. Some of them disappeared, others changed their biological properties allowing to include in their life cycle a still wider range of suitable hosts — the carriers and vectors as well. Polyhostal forms appeared, capable of dissemination over considerably large areas and capable of becoming members of different ecosystems (Galuzo 1976).

Quite a special role was allotted to domestic animals. Domesticated animals imported new causative agents into new biogeocenoses they contacted and vice versa, themselves became here a further link in the chain of circulation of original pathoergonts. In the present paper we shall not touch upon the enormous complex of problems of natural focus diseases afflicting domestic animals themselves, but shall only take account of their role in human natural focus diseases. We may assess them from two aspects. The first is the influence of animals on biogeocenosis itself, when the latter is subjected to considerable disturbance and marked changes due to pasturing, which in extreme cases may lead to complete devastation of landscape, as proved to be the case in some Mediterranean regions. As a result of such a direct disturbance of vegetation cover are secondary changes in the settlement by animal and plant species, creating quite different biocenoses. Numerous and spatially concentrated herds are also the factor which contributes to the maintenance and existence of high populations of hematophagous arthropods — the vectors of various diseases. The second aspect is the inclusion of domestic animals in the circulation of pathogenous agent. Sometimes their role in this circulation is negligible, but sometimes domestic animals may become, as far as their biological properties are concerned, equal to initial components of a natural focus and are capable of

¹A term proposed by Pavlovsky (1965) instead of "pathogen" which may suggest some genetic relationship not necessarily included in studies of the theory of natural foci of diseases.

disseminating the causative agent beyond the boundaries of the wild donors' range during their vagaries or intentional transfer. Thus they may become the source for irradiation of pathoergont in free nature and lead to formation of new natural foci existing for periods of different duration.

The most extreme stage of natural landscape cultivation by man is its transformation into more or less homogenous human settlements during the process of urbanization. Such human activity results in the adaptation of most various species to a new environment and a phenomenon called synanthropization (Rosický and Kratochvíl 1953) or domiciliation of animals (Audy 1965). The degree of synanthropization is different. Some organisms have adapted themselves only to outbuildings in the outskirts of human settlements, others also live inside settlements and yet others have transferred as close to man as his habitation. Synanthropic animals may be divided into eusynanthropes which regularly inhabit human settlements and hemisynanthropes which temporarily or occasionally do so, due to their large ecological valency. The degree of synanthropy in many species is not stable, changing in particular years and especially in various parts of their range of distribution. The tendency towards synanthropization embraces still more animal species and it is a phenomenon which is evidently in full development. Particularly adaptable proved to be many species of small mammals, birds and arthropods, namely the organisms of primary importance as carriers, reservoirs and vectors of natural focus diseases. Due to the fact that the lines of division between synanthropic and exoanthropic animals are not clear-cut and frequent contact occurs between them, either direct or through their parasites, there is a possibility of anthropourgic natural foci advancing to the close vicinity of and at the next stage inside human settlements. The infection may be thus transmitted through this chain from exoanthropic animals via hemisynanthropes to man. The next stage takes place if the causative agent is capable of circulating among natural components of urban environment without its repeated importation from outside. In such a case independent, separate foci within the settlements are created which may be called synanthropic natural foci.

The phenomenon of natural focality has in recent decades become more significant in subsequent cultivation of territory and in changing patterns in the transmission of arthropod-borne diseases under anthropogenic conditions. Changes provoked by man in biotopes cause new epidemiological connections. Particularly under conditions of high urbanization they lead in some cases to the increase of epidemiological danger. Changing patterns in relationships in the system biotope-pathoergont-vector-vertebrate host showed, on the basis of our experiences from Central Europe, a new epidemiological significance of the development prognoses of some natural focus diseases such as TBE, leptospirosis, various mycoses, toxoplasmosis, meningeal amebiasis, or diseases caused by arthropods.

The above mentioned aspects should be also taken into account in planning the program of surveillance of vectors and vertebrate reservoirs, including faunal surveys, ecological investigations, knowledge of social conditions, estimation of natural foci and their biotic and spatial structure, analysis of all data acquired and evaluation of anti-epidemic measures (Rosický 1976).

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Section 10: Agricultural Entomology and Pest Management

Systems Approach to Pest Management

Organizer and Moderator: P.L. Adkisson (USA)

The Strategy and Tactics of Integrated Pest Management

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ABSTRACT

The practice of pest management is, for evident reasons, essential to the future and accordingly deserves top priority. This long-term approach, which is expensive, calls for international collaborative efforts. It is part of applied ecology, relying heavily on the significance of pest and natural enemy population densities in terms of threshold values. Defining economic thresholds leads to proper cost/benefit evaluation, examples of which are given.

The complexity of possible interferences determining population levels necessarily calls for the use of models and computer tactics. It is essential that multi-disciplinary teams of specialists including agronomists, economists, breeders, soil scientists, plant protection and storage scientists and others reach agreement facilitating harmonized action which could be reflected in relatively simple guide-lines likely to secure production optimization for specific crops, including rotation patterns.

The Consultative Group on International Agricultural Research, co-sponsored by FAO, United Nations Development Program, and the World Bank has undertaken such collaborative work for various crops, particularly for the benefit of developing countries, by encouraging the activities of 6 international agricultural research centres.

Pest management requiring proper mobilization of all available expertise is increasingly regarded as the only logical future approach in crop protection and will necessarily result in the establishment of the mentioned guide-lines. The way in which international organizations can help in implementing the enormity of the task that lies ahead is shown.

Efforts towards optimization of production through agricultural practices including monoculturing, reduced tillage, use of high yield, genetically uniform varieties and increased use of fertilizers have created many new crop protection problems which remain partly unresolved and are likely to increase reliance on chemical technology.

Such a situation gives rise to concern also in countries disposing of sophisticated plant protection systems because of the possible breakdown of chemical technology.

Fears of this kind have been expressed this year in the United States by the National Academy of Sciences which warned that future agricultural productivity is threatened (Carter 1976). Three developments are considered by NAS to be of particular concern in challenging the effectiveness of pesticides: appearance of genetic resistance in major insect pests; disruption of antagonisms; and increased constraints on the use and development of pesticides by laws and regulations in the interest of environmental protection and occupational health and safety.

In the face of this threat, the NAS study group recommended that substantive inputs should be made for the development of ecologically based integrated control strategies.

When considering the huge investments placed by the United States in various ongoing pest management projects (Klassen 1975), it can be expected that the new impulse shall have far reaching effects on crop protection strategies.

In developing countries where the crop protection structures are often inadequate, introducing a new technology often been disruptive because the investments could not be adequately safeguarded. Difficulties in technology transfer and the lack of proper assessment of ecological and socio-economic conditions prevailing in the recipient country appeared to be a further serious obstacle. A greater part of the limited impact of the Green Revolution must be ascribed to these insufficiencies.

In Pakistan, the initial promise of the introduction of new dwarf varieties and the impact of the Green Revolution have not been sustained and agricultural productivity remains disappointingly low. Drastic reduction in the diversity of crop plants brought about by widespread use of new varieties created new problems (Boulter and Muhammed 1976).

Difficulties of a similar nature were encountered in Peru and Bolivia when introducing monocultures (Gross and von Baer 1976). The growth of population and the need for rationalization of agriculture towards specialization in one crop economies in various regions has, in addition, increased vulnerability to weather.

These few reflections showing the trend towards high productivity for economic and political reasons and the concomitant dangers in developed countries on the one hand and the relative weakness of impact resulting from insufficiently supported technologies in developing countries on the other hand are striking enough to indicate where the top priority in research has to go. Biologists who saw far ahead of their time have anticipated long ago the need for an ecologically sound approach in crop protection which on the long run is the only defensible one.

Integrated Pest Management and its Impact on Production Optimization

Remarkable studies on principles, tactics and strategies of pest management of insects and mites made by 17 contributors are contained in the book recently edited by Metcalf and Luckman (1975); it is therefore superfluous to enter here into these considerations.

When referring to the number of biotic and abiotic parameters which have to be considered for the proper implementation of pest management at the crop level and in view of the high scientific and technological content which is inherent in such programs, it becomes obvious that these key production elements united for control optimization have also a unique value for crop production optimization. The integration of available data meets with considerable difficulties because there are still important gaps in the understanding of the interaction of the eco-physical environment which control productivity in plants. This is to a large extent also true for interactions between pests and plants which means that man-made changes in the agro-ecosystem may result in conflicting situations. Thus, cultural measures, including the use of resistant varieties, fertilization, water management, crop rotation, soil tillage, timing of sowing, planting or harvesting, pruning and thinning may have a containment effect on certain pests and favour the development of others.

In addition, many of the cultural measures are imposed by economic constraints or weather and are therefore not likely to be manipulated as will be shown in the following example.

Case-history. Fungus diseases in cereal growing and cultural techniques.

In the United Kingdom, interest in growing crops without ploughing was generated and in a way imposed by recent increases in labour and fuel costs (Yarham and Hirst 1975). By 1973 about 400,000 ha. of cereals were being grown without ploughing and cereals occupied about 1/3 of the 100,000 ha. of crops drilled without prior cultivation on fields sprayed with paraquat.

Furthermore, practicability plays an important role when introducing new systems. Reduced cultivations and especially direct drilling have the advantage of being quick compared to ploughing so that brief dry spells can be utilized by the farmers. This encourages early drilling and, as a consequence, early sown crops emerge when vectors and spores are still plentiful and temperature high enough to encourage infection and incubation. As a consequence, early sown winter oats have more barley yellow dwarf virus and yield less than crops sown later (Plumb 1974). At Rothamsted, plots without insecticide yielded most when not sown until November. However, the significantly highest yield was obtained in this case by sowing in September, after phorate granules applications and followed by a menazon spray in May (Table 1).

While the costs of the pesticide and its application can be appropriately calculated, the convenience of practicability can hardly be expressed in monetary terms.

Table 1.—Effects of insecticides and their times of application on yield of winter oats sown on different dates (Rothamsted 1972-73), simplified from Plumb (1974)

Date of sowing	25 September	26 October t/ha	23 November
Treatment			
Nil	4.90	4.57	5.23
Phorate (P)	5.25	5.03	5.04
Menazon (M)	5.21	5.01	4.99
	5.46	5.18	5.08

The change from ploughing to non-plough tillage may also influence *Gaeumannomyces graminis* (Sacc.) Arx and Oliver, which is the most important soil borne pathogen on cereals growing in the UK. There are, however, so many interacting factors varying from field to field according to soil type or cropping history, or from year to year, that it remains difficult to establish any consistent pattern of effects of the techniques on disease incidence (Yarham and Hirst 1975).

These examples are given to illustrate how simple a statement on cultural method is in relation to pests and how difficult its economic assessment remains in each individual case because of still lacking epidemiological data.

Case-history. Leptohylemia coarctata (Fall.) Wheat bulb fly in cereal growing, environmental problems and period of sowing.

The introduction in the mid 50's of aldrin, dieldrin and heptachlor for treating winter wheat seeds led to the deaths of large numbers of grain eating birds and further evidence of wildlife casualties led to the withdrawals of aldrin and dieldrin for which the 2 alternatives, chlorfenvinphos and carbophenothion were used (Hamilton et al. 1976).

However, in 1971, and during the winter 1974/75, the greylag goose, *Anser anser* died from carbophenothion treated grain which remained on the soil surface after sowing. The reasons for this were the wet conditions which prevented sowing at the usual time, and in January seed was broadcast sown followed by discing. Under these conditions considerable amounts of treated grain was left on the surface. Thus, withdrawal of aldrin and dieldrin is resulting in the increase of more acutely toxic but less persistent organophosphorous alternatives, and it is not yet clear if this change will result in less overall harm to wildlife.

In any way, the solution to these incidents is certainly to be found in a better understanding of the wheat bulb fly biology which will help reduce pesticide use. Adverse climatic conditions may indeed completely upset a cultural practice considered to be safe and economic.

Systems approach

The example provided by Giese et al. (1975) in Fig. 1 showing the computerized program review chart for alfalfa pest management program considers practically all major elements exerting an influence on the plant. It is meant to take advantage of increasingly detailed research continually adding to information on the components of agricultural systems. The final goal being certainly to provide farmers with simple recipes and predictions of effects of adopted measures. According to Ebersohn (1976), "the system simulation approach is commended as a methodology worthy of consideration to complement other, ad hoc procedures in assembling information purposefully and in guiding scientists, farmers and other agricultural bodies as to where their priorities lie".

In any pest management approach the knowledge of economic thresholds for individual pests is a prerequisite. It is, roughly, the value of the loss expressed in monetary terms accruing from the pathogenic organism which is in balance with the costs resulting from action taken to prevent this loss (Steiner 1976). Therefore, the following values have to be determined: 1. quantity of pathogens causing the damage (e.g. population density); 2. relation between quantity of the pathogen and the extent of monetary losses; 3. costs inherent in preventing the damage.

The economic threshold may thus be changing from one year to another especially in consideration of the variability of the commodity prices. It clearly reflects the cornerstone of any crop protection action and includes necessarily also ecological considerations. Without threshold values crop protection remains guesswork. Even temporary and rough evaluations of these values may considerably change the protection pattern.

Once such thresholds are available, pest management can be envisaged in accordance with the general scheme represented in Fig. 2 (Ruesink 1975) which may be refined according to the needs and completed by mass flow models of the crop with environmentally and physiologically controlled rates of flow.

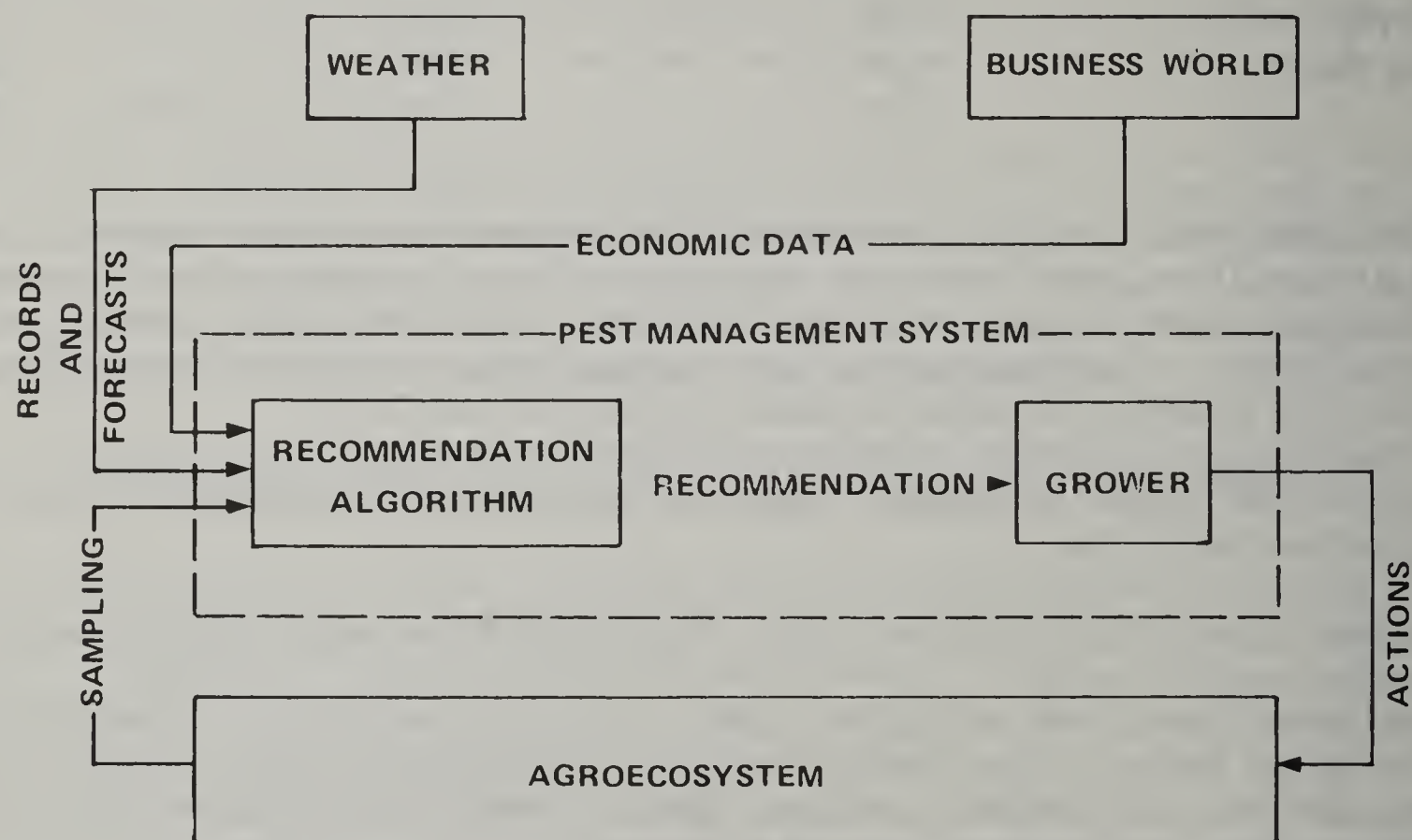


Fig. 1. –Program review chart for alfalfa pest management program, simplified from Giese et al. 1975.

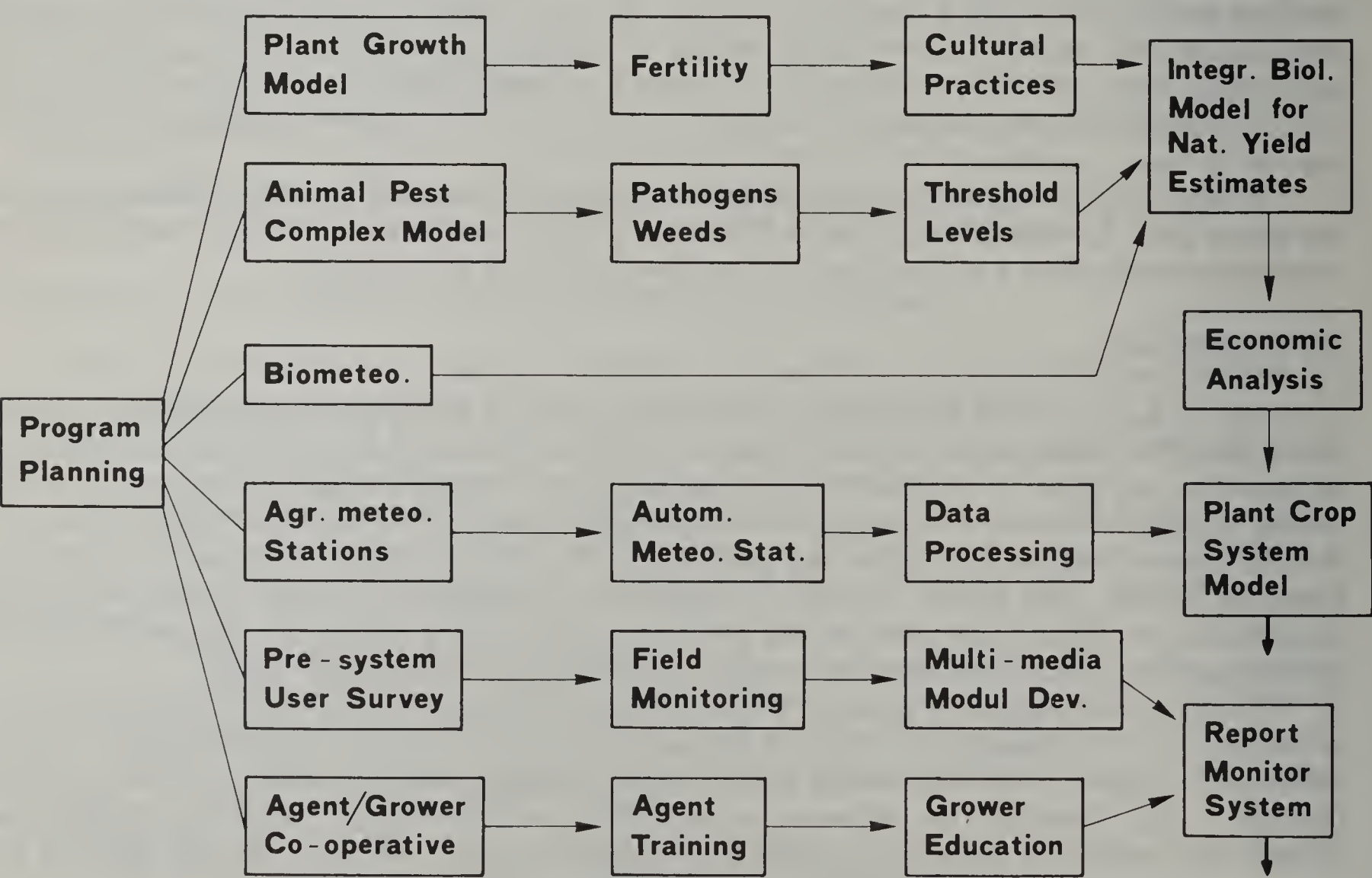


Fig. 2. –Diagram showing how pest management operates at the grower level (Ruesink 1975).

It has been stressed that the various parameters needed for the implementation of pest management correspond to those which are basic for any crop production optimization. Since collecting data which are essential for effective decision making processes is secured through real time pest control information networks, which are increasingly backed by expensive computers, it seems logical to take better advantage of this information. The practical implementation of such a project could be assured in Agricultural Research Centres and would be reflected in relatively simple guide-lines on good agricultural practices. This interdisciplinary approach could alleviate many inconveniences such as using inappropriate rootstock/cultivar combinations which, for instance in citrus growing, are detrimental with regard to susceptibility to many dangerous diseases. Guidance would be provided on cultural methods *sensu lato* so as to meet the basic requirements of pest management, with due consideration of the priorities.

Consideration to this interpretation of good agricultural practices has been given earlier in the frame of International Organization for Biological Control (IOBC)/West Palaearctic Regional Section (WRRS) and European and Mediterranean Plant Protection Organization, and OECD discussions while its proper implementation is initiated at Stuttgart in vegetables (El Titi and Steiner 1975) and pome fruit (Steiner 1975, pers. comm.). Similarly projects are ongoing in Switzerland (Favre 1975, pers. comm.) in fruit growing.

Conclusions and Outlook

The need for improved collaborative action between the various disciplines involved in crop production, processing, storage and marketing in view of production optimization has been repeatedly stressed in recommendations issued by plant protection conferences. However, little seems to have been implemented by individual countries along these lines except perhaps in places where pest management systems are operational.

It appears that in many countries there is little contact between crop protection specialists and agronomists, the latter being still of the opinion that protecting crop with pesticides is cheap and easy. This attitude may also have retarded progress in the International Agricultural Research Centres sponsored by the Consultative Group on International Agricultural Research (CGIAR) and which spearhead research and training mainly for the benefit of developing countries. Although the research programs are tackled by multidisciplinary teams of scientists including plant breeders, soil scientists, agronomists, entomologists, pathologists and others, these latter two disciplines were not sufficiently covered in the initial stage, which brought about the already mentioned difficulties.

Appropriate adjustments and retargeting of research priorities have been made since then and it appears that for instance in the International Rice Research Institute (IRRI), working on rice, top priority in research goes to plant protection. IRRI's varietal improvement team are concentrating on the search for genetic resistance to a wide range of pathogenic organisms, including rice blast, bacterial blight, bacterial leaf streak, grassy stunt, tungro virus and the insect carriers of the last two (Anonym. 1974).

Pest management systems are likely to be successful only if they rely on good agricultural practices, as stressed in the 1976 report of the National Academy of Sciences. This approach is now facilitated by the considerable amount of parameters made available for crop protection and which have to be optimized.

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The Utility of Systems Analysis Techniques in Pest Management and Crop Production

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ABSTRACT

Pest modelling in the past has suffered from being too general in focus and from paying insufficient attention to the link between populations, damage and cost. Recent work by the Environmental Management Unit has attempted to correct this omission. A model of pesticide resistance has been developed which demonstrates the critical importance of migration rates and density dependence. Extension of the model to include resistance costs indicates that the best strategies remain the same but costs increase and suggests that in the face of varying pest numbers the best strategy may be to aim at a constant damage level. Specific models of the sugarcane froghopper (*Aeneolamia varia saccharina*) and the cattle tick (*Boophilus microplus*) have been developed using the Leslie matrix and used to increase understanding of the population dynamics and for initial explorations of control strategies. However models of this form are not ideal for stimulating the feedback between modelling and field experimentation. Finally attention has been given to the objectives of systems analysis and the need to produce models which suit farmers requirements. A Bayesian approach has been found useful in illuminating situations where risk considerations are important.

Four years ago, at the XIVth International Congress of Entomology, I presented a paper (Conway 1973) which reviewed experience in pest modelling in the decade since K.E.F. Watt's pioneering work of the early 1960's. On this occasion I will not attempt another comprehensive review, but instead will focus on the work of my colleagues and myself in the Environmental Management Unit at Imperial College, describing where progress has been made and indicating where some of the problems still lie.

I believe we are long past the time when general or theoretical statements extolling the potential virtues of systems analysis in pest management have any valid impact. The worth of the approach has now to be demonstrated by the work of the ten or so systems teams currently working on specific problems in different parts of the world. Partial reviews of the field have recently been provided by Ruesink (1975, 1976) and the work of Kiritani, Gutierrez and others is well described in this Symposium. However, I wish to draw attention also to the excellent systems work of Rabinovich (Rabinovich 1971, Rabinovich and Dorta 1973) on the triatomid vectors of Chagas disease and to the pathfinding studies of the spruce bud-worm of Holling and his co-workers (Holling et al. 1975, 1976) which are not represented at the Symposium.

At the last Congress I levelled three criticisms at the existing mathematical models. First, I felt that too much effort had gone into building generalised pest models; only rarely had these demonstrated other than the obvious or the trivial. Second, the few models of specific pest situations which had been produced were deficient because they ignored the key relationships between pest numbers and damage and between damage, control and cost. Third, few of the general or specific models had been formulated in a way which would initiate the process of interaction between

experiment and model building. This interaction is critical to the production of relevant and useful models.

As is evident from this symposium attention has now turned to building better specific models, but in this paper I refer first to a generalised pest control model which examines the phenomenon of pesticide resistance and does provide useful and original insights. Second, I discuss the structure of pest population models and their utility, particularly in relation to experimental work. I then describe how the economic and ecological aspects have been linked for a specific pest problem. Finally I discuss the objectives of pest control models, referring to some of the experiences of workers engaged in applying systems analysis to agricultural production in general.

Insecticide Resistance

Somewhat surprisingly no one has attempted, until recently (Hueth and Regev 1974), to provide mathematical models which describe the development of insecticide resistance in pest populations. The problem of resistance is now very serious. A wide range of both chemical compounds and pest species are involved (Brown 1971). At regional and national levels we urgently need strategies of control that will delay the onset of insecticide resistance and at the farm level, tactics are required that will minimise the additional costs of pest control that the development of resistance imposes.

Two recent papers by Hugh Comins of our Unit have made significant advances. In the first paper (Comins 1976) he considers the interaction of five critical parameters:

1. The degree of dominance of the resistant genes
2. The intensity of insecticide application
3. The initial frequency of the resistant gene in the population
4. The amount of insect migration into and out of the treated area
5. The degree of density dependence in the population.

Comins postulates a treated and an untreated population linked by migration (Fig. 1) and develops a simple deterministic, Mendelian model based on a single allele for resistance. He assumes

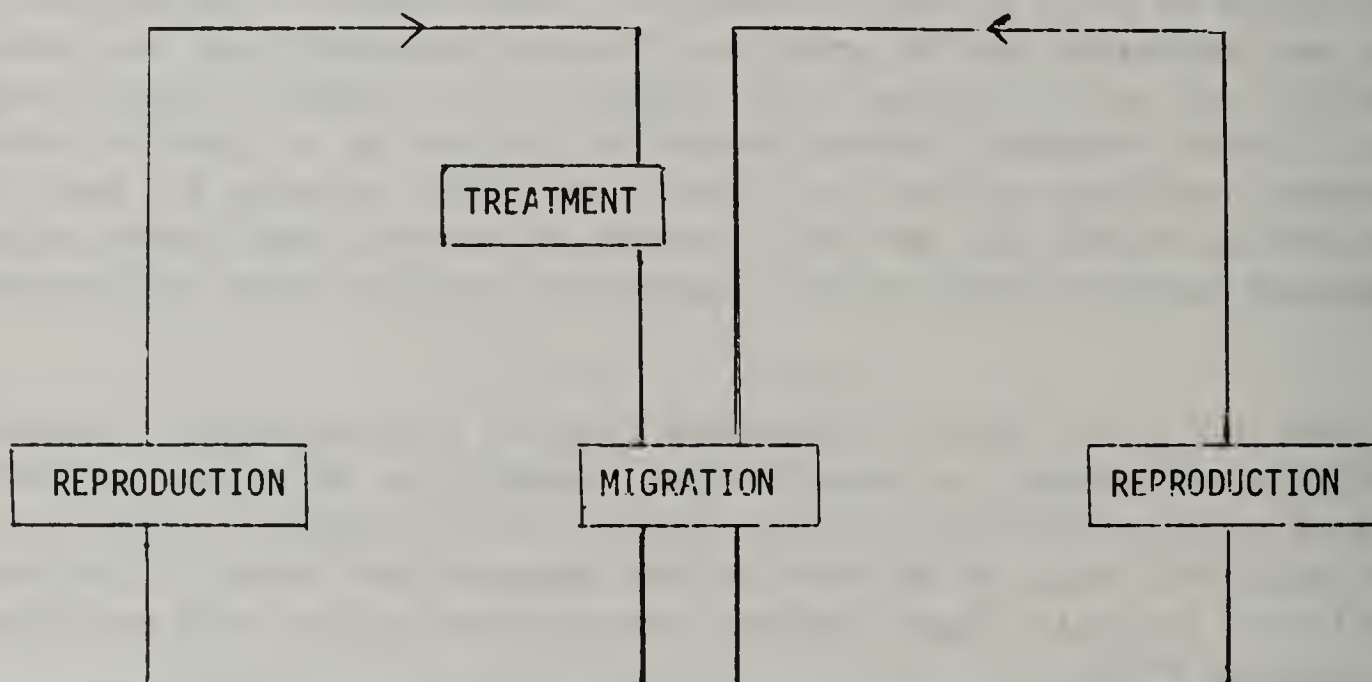


Fig. 1. —Insecticide resistance model Diagram of the interacting treated and untreated populations (After Comins 1976)

initially that the size of the untreated population is infinitely large and that the populations are regulated in a perfect density dependent fashion i.e. $b = 1$ in the equation:

$$N_{t+1} = \lambda N_t^{1-b}$$

(May et al. 1974). Under these conditions he shows that the resistant gene frequency in the treated population may have three equilibrium values. Two of these are stable: one low equilibrium point where the population is mostly susceptible and one high where the population is mostly resistant. There is a critical value of the migration rate below which a sudden transition occurs to the high equilibrium frequency (Fig. 2). With more dominant genes the size of the jump is reduced. In the more realistic case of a finite size for the untreated population the resistance gene always eventually

becomes fixed although Comins shows by simulation studies that in the short term the gene frequency may still approach a low equilibrium value for sufficiently high migration rates.

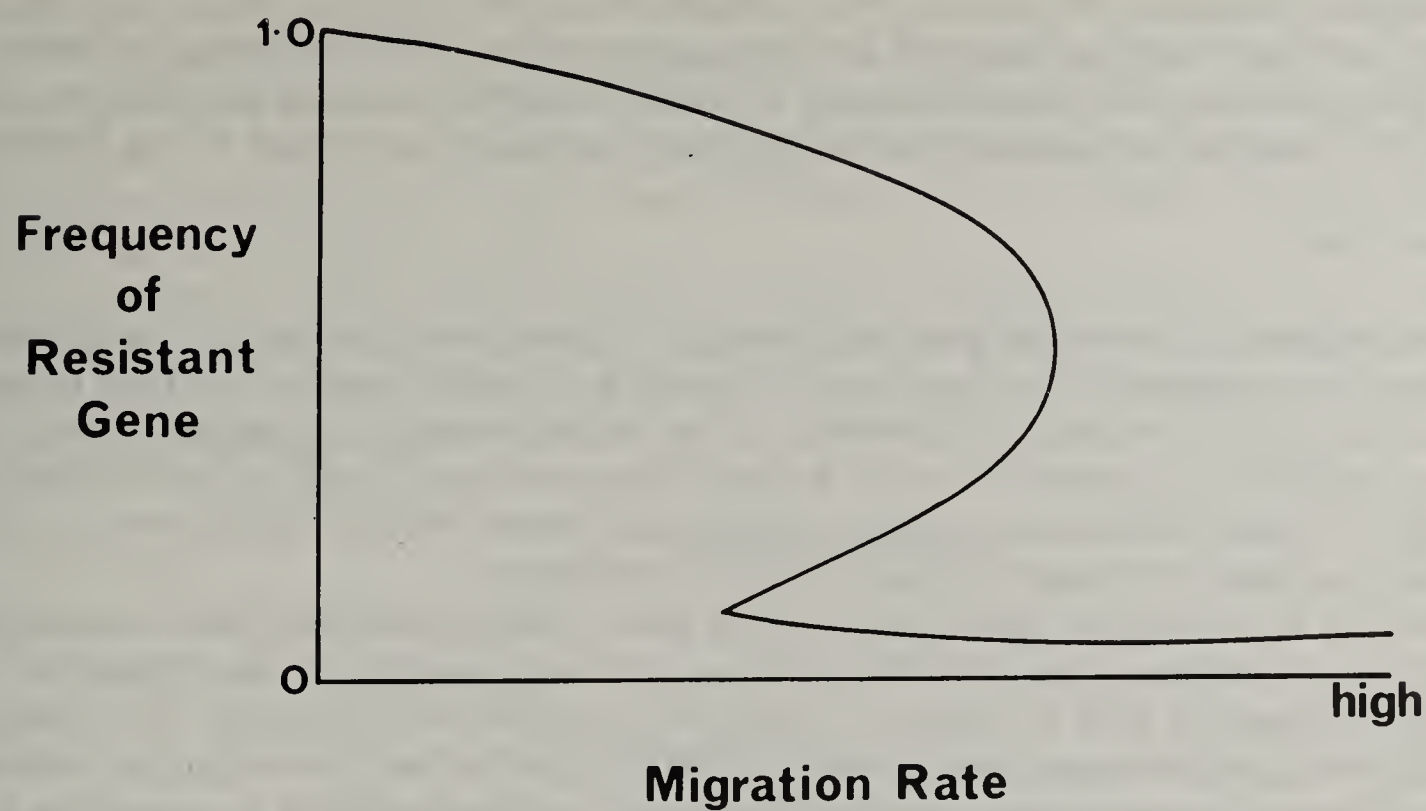


Fig. 2. –Effect of migration rate on the frequency of resistant genes in an insecticide treated population. The initial gene frequency in this case was assumed to be .04 (After Comins 1976)

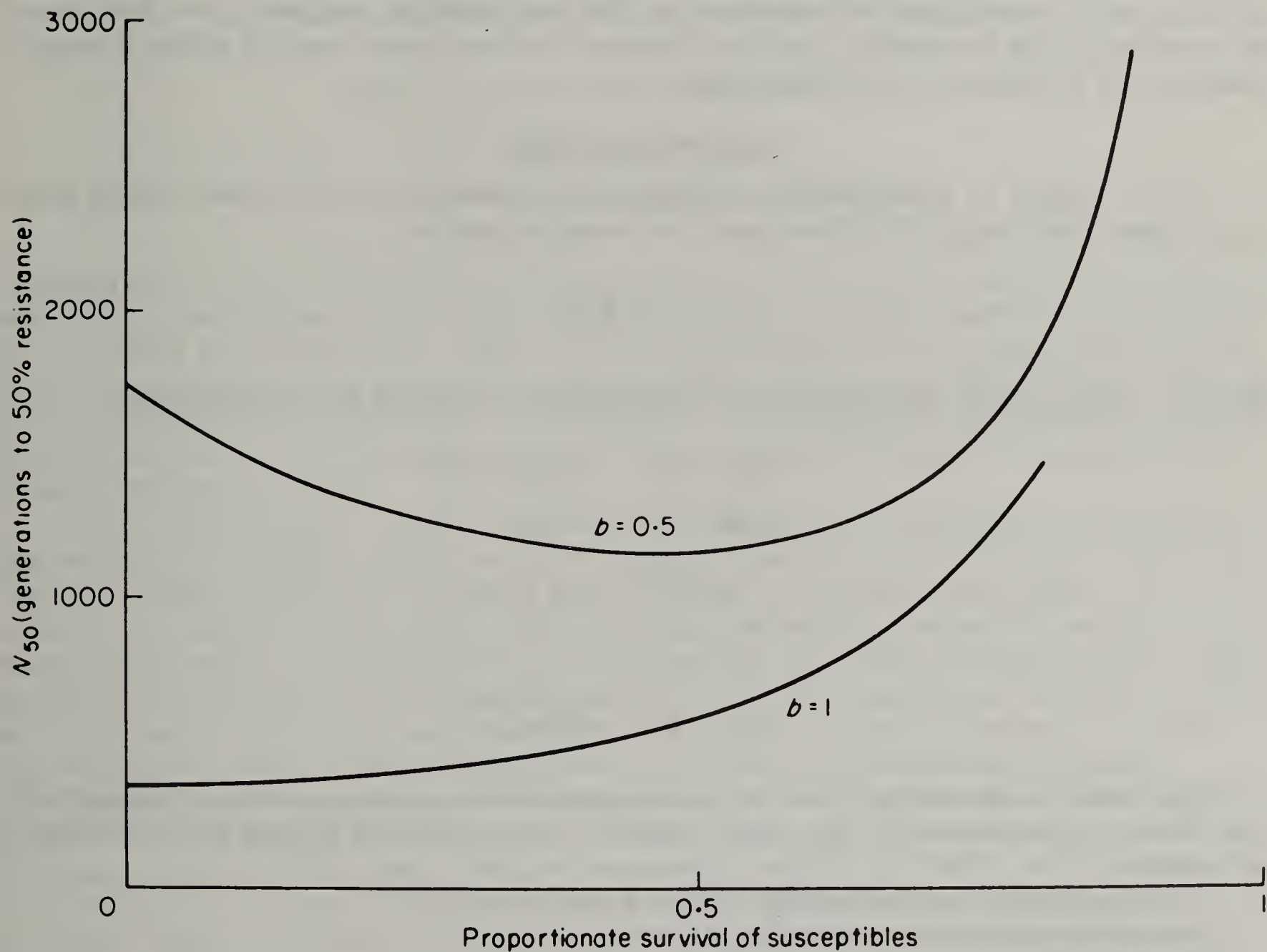


Fig. 3. –Effect of density dependence on the resistance time (number of generations required for gene frequency to reach 50% in an insecticide treated population. $b=0.5$ represents undercompensating density dependence; $b=1.0$ represents perfect density dependence (After Comins 1976)

Comins then explores the relationship between the degree of density dependence and the intensity of the insecticide kill. For perfect density dependence he finds that the resistance time (number of generations required for gene frequency to reach 50%) decreases with increasing kill (Fig. 3). But where density dependence is under-compensating, ($0 < b < 1$) this result may be reversed, the resistance time increasing at high and low kills; intermediate kills producing the fastest resistance. Comins concludes that for reasonable levels of density dependence, resistance may be suppressed by using highly effective, non-residual insecticides which are strictly confined to the target population.

Resistance Costs

The problem of producing practical strategies for minimising the costs of pesticide resistance is complicated by a number of factors. First, to be useful strategies have to be devised before resistance is detected; i.e. in the absence of knowledge of the initial frequency or mutation rate of the resistant gene or of whether it is recessive or not. Second, incorporation of costs in the calculations involves knowledge of a rather nebulous economic concept: the present value of the future cost of changing to a new pesticide when the present pesticide becomes ineffective.

However in his second paper Hugh Comins shows that, given certain general assumptions about the genetics of resistance, the rational strategies can be reduced to a one parameter set (Comins 1977). At this general level a number of interesting conclusions are possible. For example, Comins finds that the rational strategies when resistance cost is included become simply the optimal strategies which result when resistance is ignored but the cost of applying pesticide is assumed to be somewhat larger than it actually is. He demonstrates also that where pest numbers vary from year to year, the optimal strategy is to keep losses from pest damage at a roughly constant level regardless of the initial pest numbers each year, providing that the pests are not so few as to be incapable of causing that level of loss.

For any particular situation the precise strategy requires knowledge of the rate of selection to resistance and an evaluation of the resistance cost. But since these are relegated to the final step of the procedure, it may be possible to arrive at a reasonably robust strategy based on various alternative assumptions in the absence of precise knowledge.

Leslie Matrix Models

In our attempt to model specific pest situations, we have so far relied heavily on the Leslie matrix (Leslie 1945, Usher 1972). Here population change is given by

$$\underline{n}_{t+1} = \underline{A} \underline{n}_t$$

where \underline{n}_{t+1} and \underline{n}_t are the age class vectors of the population at time $t+1$ and t and the matrix

$$\underline{A} = \begin{matrix} & \begin{matrix} f(0) & f(1) & \dots & f(k-1) & f(k) \end{matrix} \\ \begin{matrix} p(0) \\ 0 \\ 0 \\ 0 \\ 0 \end{matrix} & \begin{matrix} 0 & p(1) & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & \dots & p(k-1) & 0 \end{matrix} \end{matrix}$$

The Leslie matrix has the merit of describing population change in a neat and conceptually clear manner. Construction of the matrix depends upon three well defined sets of biological information:

Development time which determines the size of the matrix

Fecundity which gives the values for $f(x)$

Survival and migration, which give $p(x)$.

We used a model of this kind in our studies of the sugar-cane froghopper *Aeneolamia varia saccharina* (Dist.) which have been carried out in conjunction with Dr. A.B.S. King of the Caroni

Research Station in Trinidad (Conway et al. 1975). Fecundity and development times were obtained from laboratory and field experiments and the matrix model fitted to a variety of field records by adjusting survival and migration rates. Figure 4 shows field records and the model fit for the four consecutive broods in a sprayed field in 1972. We have found that this kind of procedure is often very illuminating. For example, in the set of data depicted here the discrepancy between the model and the field record toward the end of the third brood is of interest. We believe the discrepancy can be accounted for either by density dependent adult migration or by density dependent competition between the nymphs for feeding sites on the sugar-cane roots. The model fitting procedure suggests hypotheses which can be subsequently tested.

We have also used a Leslie matrix model to describe population change in the cattle tick *Boophilus microplus* on cattle in South East Queensland. This work is being carried out in conjunction with Dr. R.W. Sutherst of the C.S.I.R.O. Here we have divided the population structure into week, rather than day, age classes

$$\begin{array}{rcl}
 & & \text{week age classes} \\
 n(0)_t - n(4)_t & \text{eggs} &) \\
 n(5)_t - n(8)_t & \text{larvae} &) \text{ in pasture} \\
 n(9)_t - n(11)_t & \text{parasitic ticks on cattle} & \\
 n(12)_t & \text{adult females in pasture} &
 \end{array}$$

The model is more complicated than for the froghopper because of the proven existence of density dependent competition of the parasitic larvae on the cattle. This has the form

$$n(9)_t = a [2\ell p(n(5)_t + n(6)_t + n(6)_t + n(7)_t + n(8)_t)]^{1-b}$$

where ℓ = larval weekly survival rate

p = weekly host finding rate

a, b are density dependent coefficients

Estimates of the values for development, fecundity and survival have been obtained from a variety of published and unpublished sources. Figure 5 shows the pattern of tick population growth produced by the model for European and Zebu type cattle. This seems to accord reasonably well with experience in South East Queensland. In practice European cattle are killed well before tick numbers reach the levels shown in the figure. The difference in tick population numbers between the two cattle types is due to the much greater degree of density dependent competition among the parasitic larvae on the Zebu type cattle.

These matrix models provide a convenient starting point for exploration of the effects of different control strategies. In the case of the cattle tick we have used the model to explore the effects of different timing of insecticide dipping against the parasitic ticks. Figure 6 shows the reduction in total tick weeks on European cattle which occurs as a result of first, second, third or fourth brood dipping. The superiority of early dipping is very clearly demonstrated. This result appears to be fairly robust: it is not qualitatively affected by differing estimates of the development rates or potential rates of increase although it is significantly affected by changes in the degree of density dependent competition and the synchrony of egg hatch at the beginning of the season.

We have found these matrix models to be useful in the way I have described: in gaining greater understanding of population processes and in our initial explorations of control strategies. Their main advantage lies in the fact that they are conceptually simple and readily understandable by non-mathematical biologists. However they have a number of disadvantages. As Martin Birley of our Unit points out, they become clumsy when density dependence processes are included and it is difficult to accommodate varying development time in the matrix, particularly when this is dependent upon density. A more important criticism is that in practice it is not easy to provide parameter values on an age class basis. Age classes may not be readily identifiable in the field or

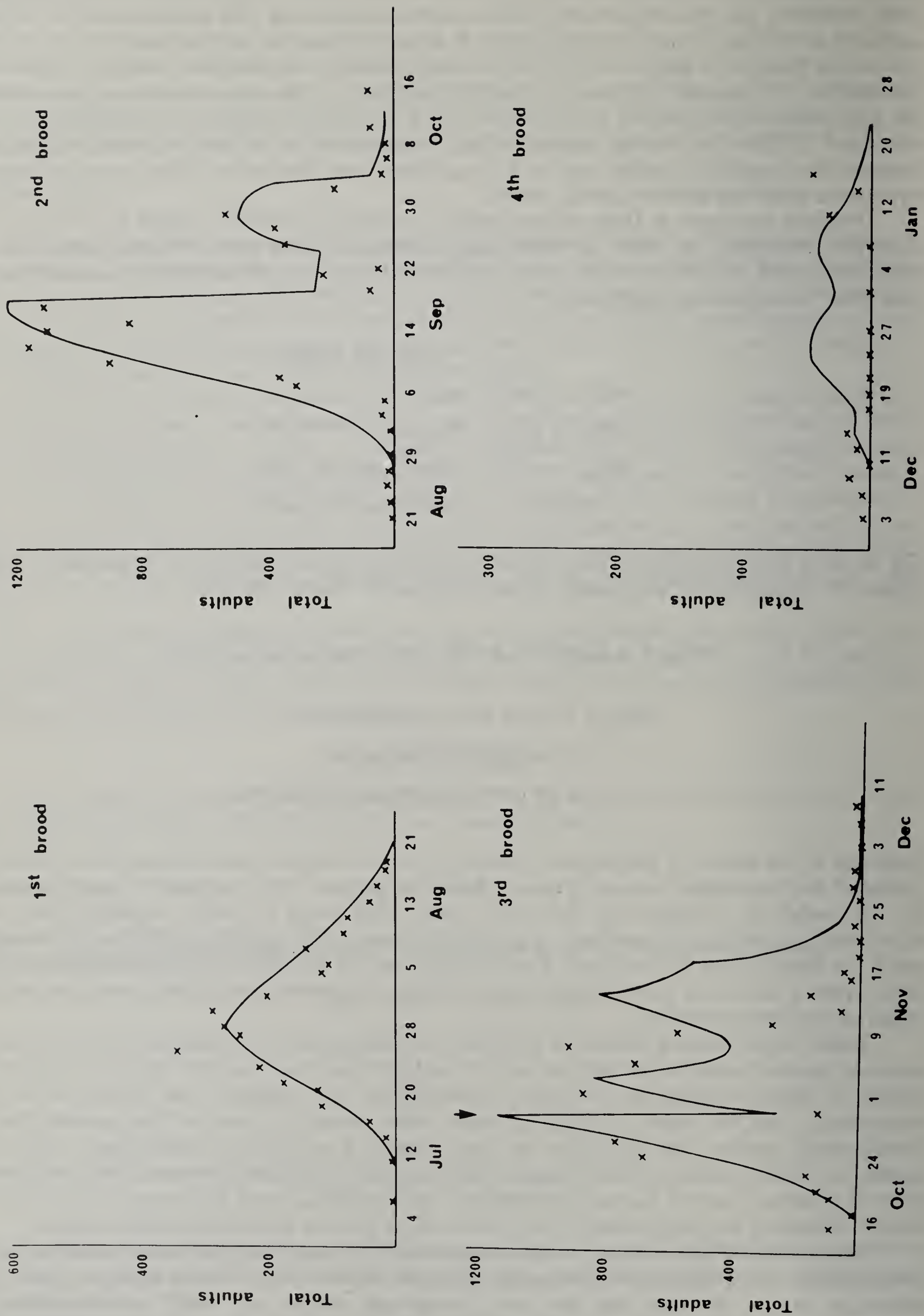


Fig. 4. —Field records of four generations of the froghopper on sugar cane in 1972 and the fitted Leslie matrix model (Conway et al. 1975)

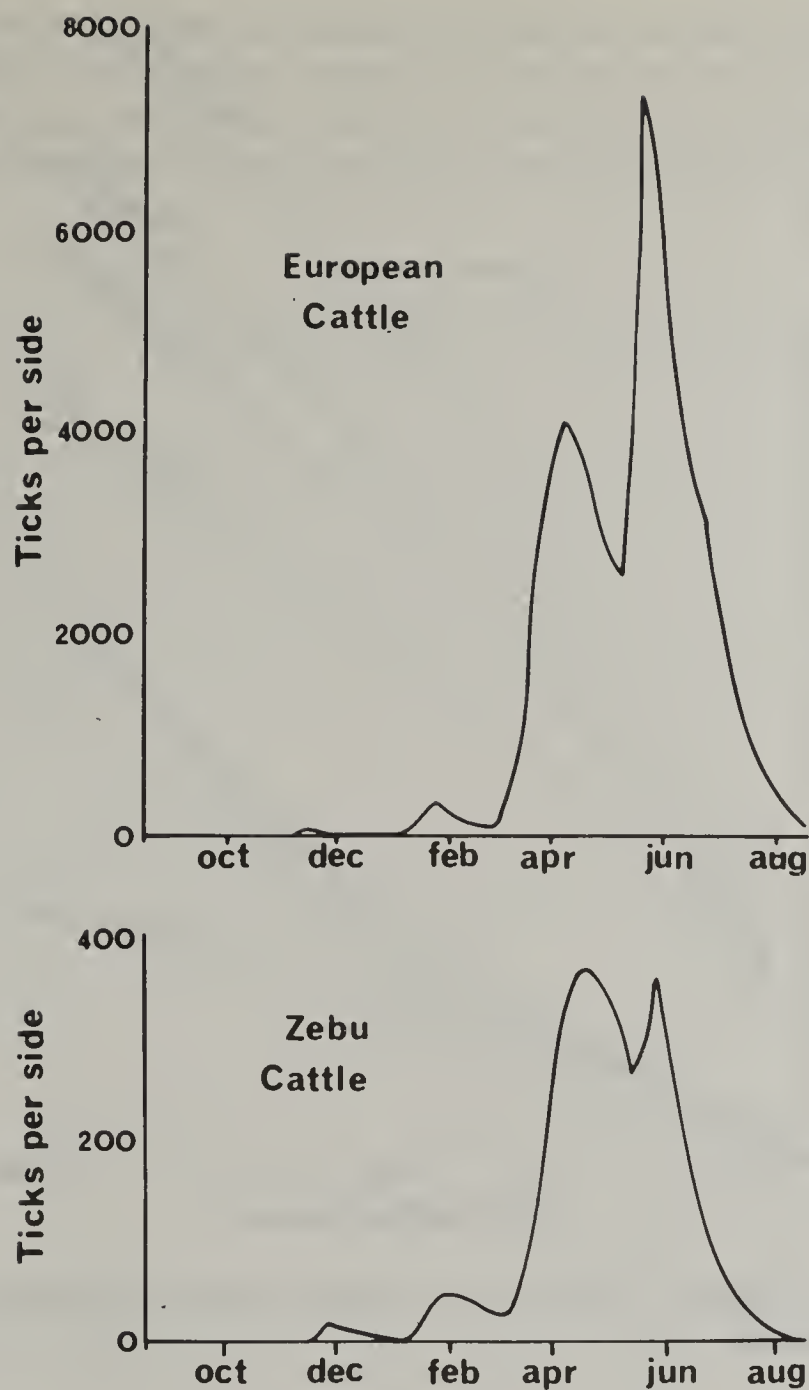


Fig. 5. —Simulations of the seasonal pattern of cattle tick populations on European and Zebu type cattle in South East Queensland.

laboratory and some parameters, particularly those concerned with survival and development, may require difficult or laborious experimentation. Leslie matrix models are thus not as effective as we might hope in stimulating the kind of feed-back between model building, experimentation and field work which we believe to be at the core of the successful application of systems techniques in pest control. Birley believes the answer lies in transfer function models which will bring the estimation and control aspects much closer together (Birley 1977). He is currently working on such models for the frog hopper and tick populations.

Population, Damage and Costs

The Sugar Cane Frog hopper

If a multi-voltine pest has little or no density dependence then the most profitable control arises from killing the population early in the season. The control problem only becomes complicated if there is a strong density dependent relationship between the different generations or if there is a complex damage relationship involving some degree of plant compensation.

In the case of the sugar cane frog hopper there is little evidence of plant compensation and the available data suggests that damage is linearly related to numbers of frog hoppers measured in terms of total adult days. But we have explored the effects on control strategies of different degrees of density dependence assuming the broods to be related by the function

$$A_{t+1} = \lambda A_t^{1-b}$$

where A_t and A_{t+1} are the numbers of adult days in broods t and $t+1$ and b is the density dependent coefficient.

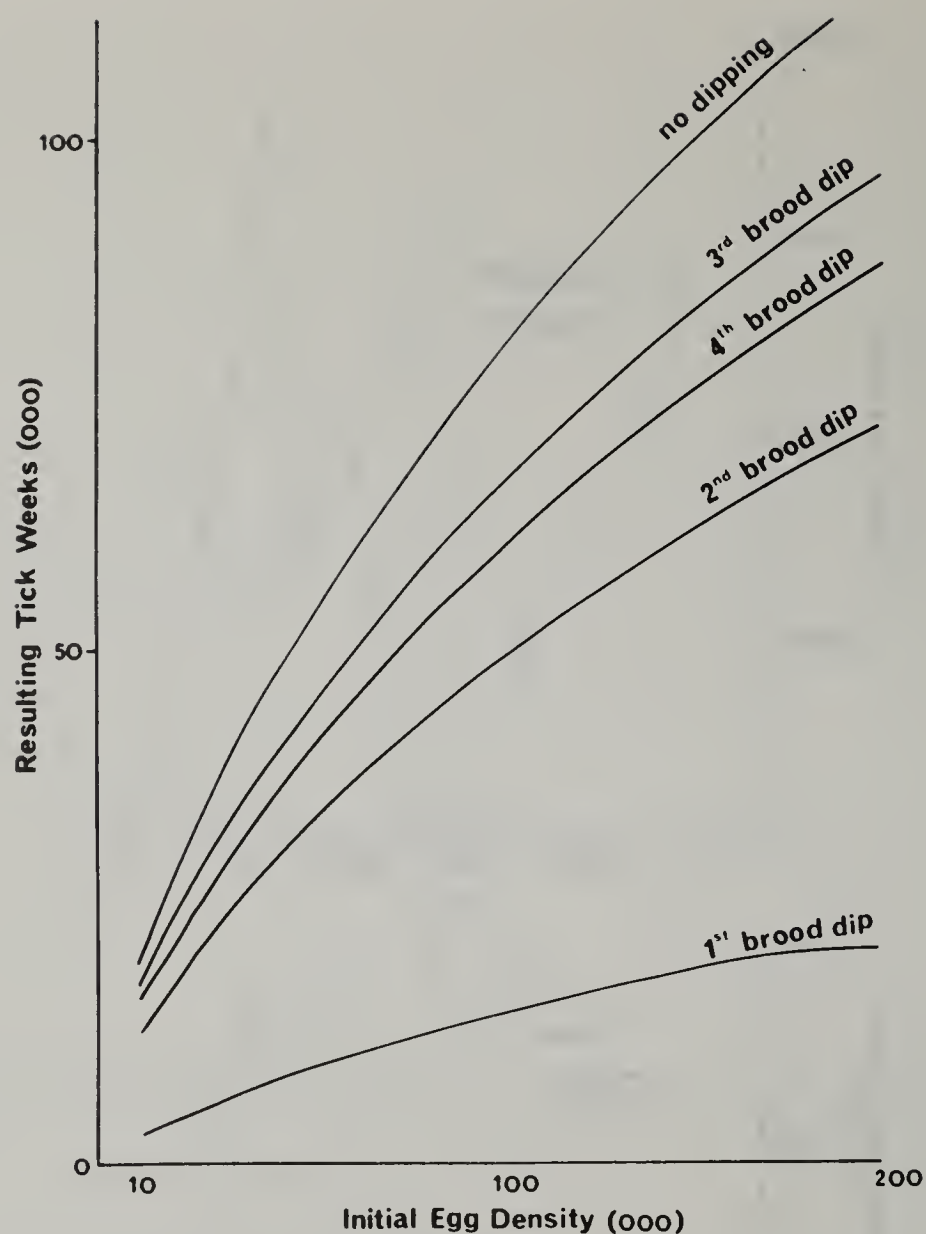


Fig. 6. —Results from computer simulation of the effect of timing of insecticide dipping on the reduction in cattle tick weeks on European cattle.

We have looked at the consequences of spraying residual and non-residual insecticides using costs which are appropriate to Trinidad conditions. Allowing for three possible sprays per brood, there are a total of fifteen possible strategies of which nine are dominant (Table 1). An algebraic relationship allows us to calculate the number of adult days removed by a single spray and it is then possible using a simple computer search technique to determine the optimal spraying strategies for a

Table 1.—Ten spraying strategies against a single froghopper brood (After Conway et al. 1975)

Strategy	Number of Sprays		Adult-Days Removed
	Non-residual	Residual	
1	—	—	0%
2	1	—	19%
3	2	—	33%
4	—	1	38%
5	3	—	43%
6	1	1	49%
7	2	1	57%
8	—	2	61%
9	1	2	67%
10	—	3	75%

single brood (Figure 7). Since the damage function is linear the net revenue curves are also linear. A strategy becomes profitable when its net revenue line intercepts the non-spray revenue line (strategy 1) and for each brood size the uppermost revenue line indicates the most profitable strategy. The arc subtended by these upper lines describes the optimal spraying policy for the range of brood sizes.

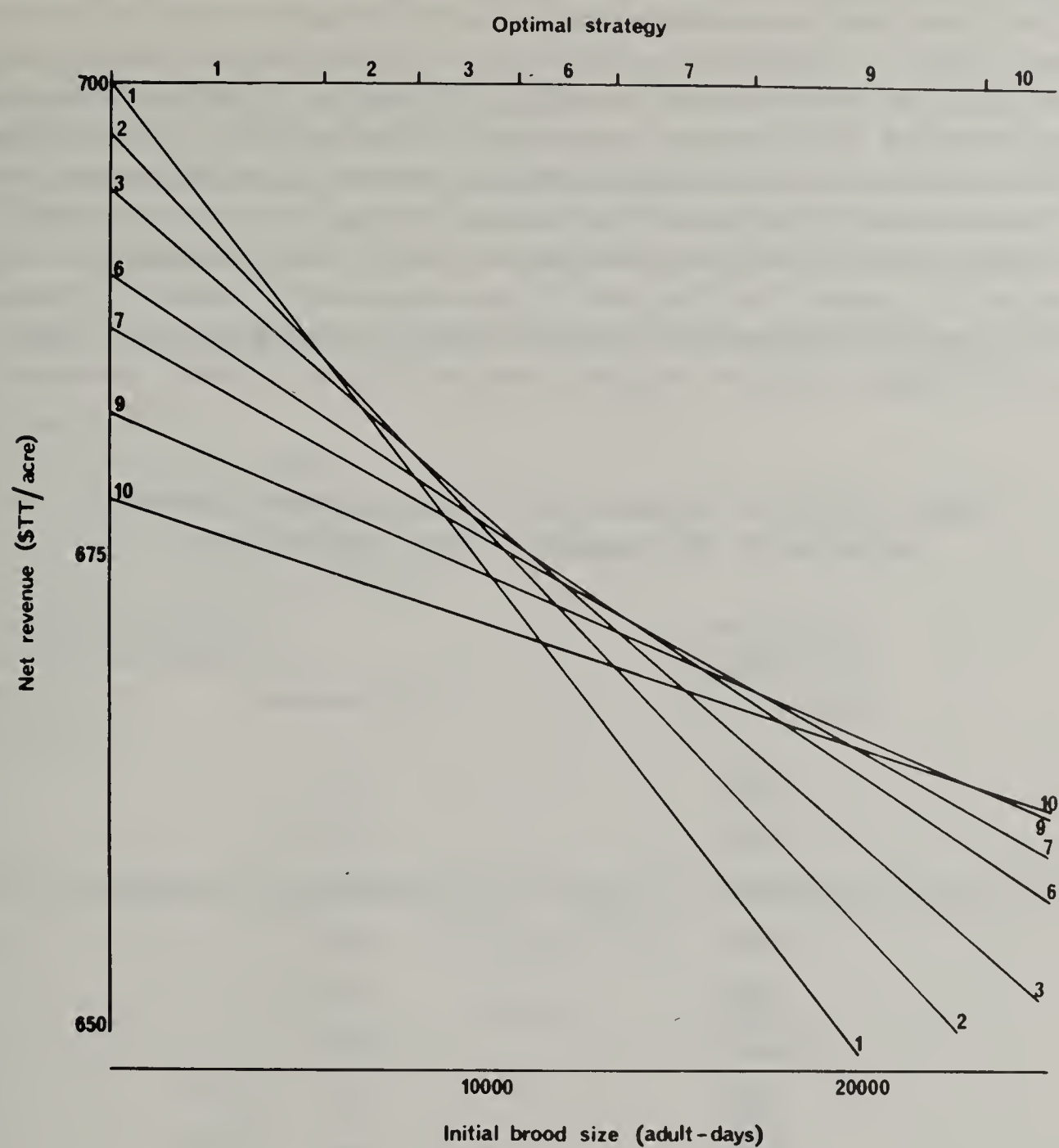


Fig. 7. –Optimal strategies for spraying a single brood of the sugar cane froghopper. The strategies are as in Table 1. (Conway et al. 1975)

The problem becomes computationally more complex however when we deal with four successive broods and we have resorted to the technique of dynamic programming to obtain a solution (Shoemaker 1973). Table 2 gives the result of this exercise and indicates very clearly the way in which optimum strategies change depending upon the degree of density dependence.

Table 2.—Optimal spraying strategies against all four froghopper broods with varying degrees of density dependence. Strategies as in Table 1 (after Conway et al. 1975)

Initial Size of 1st Brood (Adult-days)	Density Dependence											
	b=0				b=0.5				b=1.25			
	(none)				(undercompensating)				(overcompensating)			
	1st	2nd	3rd	4th	1st	2nd	3rd	4th	1st	2nd	3rd	4th
2000	7	3	1	1	1	10	3	1	1	10	10	1
5000	10	5	1	1	6	10	3	1	1	9	10	1
10000	10	10	1	1	10	10	3	1	2	9	10	1

It should be stressed that this exercise only results in a guide to the most likely rational strategies. More precise recommendations can only come about when there is greater knowledge of the actual degree of density dependence present in the population. A day to day management model would obviously require considerably more data and, in particular, would necessitate the use of a model such as the Leslie matrix or a transfer function model which accurately depicts the changes in age distribution as a function of pesticide spraying.

Comins has applied his resistance model to this analysis of the sugar-cane frog hopper. He assumes a characteristic resistance time of four and a half years and that the cost of pesticide would be doubled once resistance to the present compound is established. The optimal strategies are the same as those when resistance is not considered but the effective prices are increased. As can be seen from Table 3, where density dependence is undercompensating the resistance cost becomes large when there is a large initial population, reflecting the much heavier pesticide treatment which is required for successful control. But the case of overcompensating density dependence is more complicated, since a large initial population produces a smaller second brood and a larger third brood. The additional cost brought about by resistance thus tends to be relatively constant for all initial populations.

Table 3.—Effect of resistance on the cost of optimal spraying strategies for the frog hopper (after Comins 1977)

Density Dependence	Initial Size of 1st Brood (Adult-days)	Total Cost (\$)	
		No Resistance	Resistance
b=0.5	2000	59	59
	5000	73	77
	10000	84	99
b=1.25	2000	90	98
	5000	95	100
	10000	104	109
b=0	2000	35	35
	5000	49	53
	10000	60	75

The Objectives of Systems Analysis

In the work described so far the implicit objective has been the maximisation of profit. So defined, the problem is mathematically elegant and allows for the utilisation of classical optimisation techniques such as dynamic programming, as described above for the frog hopper. This is probably a reasonable definition of objective for the forghopper problem where the sugar-cane is being managed on a large-scale estate basis. However the experience of a number of workers attempting to apply systems techniques to agricultural production suggests that such a simple definition of objectives may be frequently inappropriate. The situation is well described by Thompson in his account of the CANFARM data system in Canada (Thompson 1975). Their experience is that farmers are rarely interested in techniques for obtaining whole farm optimisation. In practice managers of farms have a large number of identifiable objectives and many of these are in conflict with one another (Table 4).

Geoffrey Norton of our Unit has begun to consider this problem in the context of pest control decision making. He points out the importance of considering the risk position of the farmer. The simple goal of profit maximisation assumes that the farmer is risk neutral; in other words, he values each successive increment in income in the same way. But many farmers can be classified as risk averse; initial increases in income are valued higher than later increases. Subsistence farmers in

developing countries provide an extreme example. They put a much higher value on achieving each year the necessary level of subsistence than on each increment of income above that level.

In a detailed study of potato blight Norton has demonstrated the value of using a Bayesian approach to analyse a situation where risk is important (Norton 1976). Table 5, 6 and 7 summarise the essential steps in constructing a Bayesian decision matrix for a simple hypothetical case involving pest attacks in two different regions of a country. The farmer in the North who sprays every year will expect an average monetary outcome of $.4 \times 750 + .6 \times 800 = \780 and the farmer who does not spray will expect $.4 \times 200 + .6 \times 900 = \620 . By similar calculation the farmer in the South who sprays expects \$795 and the farmer who does not spray expects \$830. It is thus rational in terms of average long term profitability for farmers to spray in the North but not in the South. However, it is clear from Tables 6 and 7 that unsprayed crops experience a much greater variance in outcome than sprayed crops. Thus although in the South not spraying gives the highest overall profit, one year in

Table 4.—Some objectives of agricultural production (After Thompson 1975)

- Profit maximisation
- Fixed investment minimisation
- Working capital minimisation
- Return on capital maximisation
- Income stability and risk avoidance
- Technological excellence
- Influence in the community
- High staff wages
- Tax avoidance

Table 5.—Probabilities of heavy and light pest attack for two different regions of a country. (Conway 1976)

	Heavy	Light
North	.4	.6
South	.1	.9

Table 6.—Expected yields in lbs per acre following heavy and light pest attack on sprayed and unsprayed crops. (Conway 1976)

	Heavy	Light
Sprayed	85	90
Unsprayed	20	90

Table 7.—Expected return in dollars following heavy and light pest attack on sprayed and unsprayed crops. Cost of spraying = \$100/acre; value of crop = \$10/lb. (Conway 1976)

	Heavy	Light
Sprayed	750	800
Unsprayed	200	900

ten it will produce an extremely low return and the risk averse farmer may decide to spray every year to prevent this one in ten occurrence.

But often risk may be replaced by uncertainty. Information on the damage or control functions may be inadequate or the effect of agronomic and climatic variables on the functions may be unknown. Future prices and costs may be difficult to estimate and there are uncertainties about a whole range of other farming operations which impinge directly or indirectly on pest control. In real life farmers may thus have only the vaguest idea of the probability distribution of outcomes associated with various control strategies. Instead of seeking some ideal optimal solution the farmer may be more realistically content with one which generally satisfies a set of goals and constraints (Norton 1976). What he requires are decision rules which guide him towards such a solution.

I believe systems analysis has two clear functions in pest control: first, to define the goal and the constraints within which a satisfactory solution has to be found and second, to develop better decision rules. As in other fields successful systems analysis depends on defining correctly the key questions which have to be answered and then on choosing carefully those models which are most appropriate in answering each particular question.

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New Systems Technology for Cotton Production and Pest Management

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ABSTRACT

A general population model for cotton (i.e., any crop) – pests-weather interactions is described. Special attention is given to the similarities in mathematical form of the models describing the different trophic levels and their coupling mechanisms. The potential of incorporating recent advances in biophysical modelling of various subcomponents in each of the trophic level models is discussed. The uses of systems models in crop production-pest management are described.

Introduction

Cotton (*Gossypium hirsutum* L.) is a plant species with an indeterminate growth form, and has very interesting interactions with its different herbivore pests. The goal of many cotton production and pest management specialists has been to understand these interactions, and to develop strategies for minimizing the impact of various factors (pests, cultural & agronomic practices, etc.) on cotton yields. The problem is made difficult because cotton plants can greatly compensate for various stresses (e.g., insect herbivore damage or temporary water stress). The development of general strategies is compounded because of variety differences, regional weather patterns, pest phenology and a myriad of other problems and interactions. The scope of the problem is that of ecosystems analysis; in this case a cotton ecosystem.

Analytical Model

To be meaningful, the analysis must be realistic, yet sufficiently simplified so that the results are comprehensible and have practical utility. The goals of the analysis should be technically realistic: they should stress understanding of the fundamental, biological and physical mechanisms which determine the pattern of the crop's growth and development. The object should not be some unachievable accuracy of prediction.

The NSF sponsored Integrated Pest Management Project in Cotton (GB-34718) has now provided sufficient experience so that a conceptual mathematical framework can be developed, and so that we can now begin to see the types of information that are required to build the cotton ecosystem models. From these models will come the insights required to develop crop production – pest management strategy models.

Ecosystem models derive their components from a variety of disciplines, and it must be stressed that many of the components are still in the developmental stages. The ecosystem models must be a series of population models with the appropriate species specific physiology, behaviour and weather-related developmental factors. It is now apparent that a very generalized mathematical structure for all ecosystem population models is now available, and in a general form is reviewed by

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Streifer (1974). Wang, Gutierrez and Oster (In Press) developed a model for cotton growth and development which utilizes this structure, and have used it to couple the effects of defoliators (*Spodoptera exigua* (Hübner) and *Trichoplusia ni* (Hübner) – Gutierrez et al. 1975) and some of fruit attacking insects (*Lygus hesperus* Knight – Gutierrez et al., in press – *Pectinophora gossypiella* Saunders – A.P. Gutierrez et al., unpubl – *Anthonomus grandis* Boheman – Y. Wang et al., unpubl.). Much of the physiology used to develop the first version of the model was derived from work by Baker et al. (1972), Hesketh et al., (1971) and McKinion et al., 1974, while the conceptual framework for the population model came from detailed field experiments.

The mathematical form of the model. – Hughes (1963) was the first to develop the appropriate population model for the growth and development of insect populations in the field, but failed to recognize the underlying mathematical form (see Streifer 1974). It is essentially the same form as that used by Gutierrez et al. (1975) and Wang et al. (In Press) to formulate their cotton models. Most field population studies have used age-specific life tables (see Southwood 1968), but Hughes (1963) recognized that a time varying life table was required. In his model, he used the concept of physiological time, realistically included density dependent feedbacks, age structure, plant effects and various other components which later workers have found useful in developing their models. The simplest form of a time varying life table is a Leslie Matrix (Leslie 1947) and can be described as follows:

$$\begin{bmatrix} Mx_1(\cdot) & Mx_2(\cdot) & \dots & Mx_n \\ 1x_1(\cdot) & 0 & & 0 \\ 0 & 1x_2(\cdot) & & \\ \cdot & \cdot & & 0 \\ \cdot & \cdot & & \\ \cdot & & \cdot & \\ 0 & \cdot & \cdot & 1x_{n-1} & 0 \end{bmatrix} \cdot \begin{bmatrix} N_{1,t} \\ N_{2,t} \\ \cdot \\ \cdot \\ N_{n,t} \end{bmatrix} = \begin{bmatrix} N_{1,t+\Delta t} \\ N_{2,t+\Delta t} \\ \cdot \\ \cdot \\ N_{n,t+\Delta t} \end{bmatrix}$$

Note that $1x_n = 0$, and all $1x_i(\cdot)$ and $Mx_i(\cdot)$ are complex age specific functions determining survivorship and natality rates, respectively. For example, $Mx_i(\cdot) = f(\text{age, density, nutrition, weather} \dots)$. The influence of many of the more important factors are being studied by many groups with the view in mind of incorporating them into time specific life table models.

The continuous form of that model is

$$\frac{\partial N}{\partial t} + \frac{\partial N}{\partial a} = -\mu(\cdot)N(t,a)$$

where $\mu(\cdot)$ is a complex mortality function and $N(t,a)$ is the number density function for the organism. The simulation cotton model proposed by Gutierrez et al. (1974) and the analytical form proposed by Wang et al. (In Press) are composed of separate balance equations (models) for leaf (L), stem (St), root (Rt), fruit populations (numbers = F and mass = M) and the nutrient pool (C = carbohydrate) on a per unit area basis; not necessarily a single plant. Harper and White (1971) pointed out that plant population dynamics studies have unique problems. First there is a population of plants (eqn. 1) (ρ), and each plant has populations of parts of different ages (eqn. 2-6). These models can be written as

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} = -\mu_\rho(\cdot)\rho(t,a) + I \quad \begin{matrix} \rho(t,0) = \beta_\rho(t) \\ \rho(0,a) = \gamma_\rho(a) \end{matrix} \quad (1)$$

$$\frac{\partial L}{\partial t} + \frac{\partial L}{\partial a} = -\mu_L(\cdot)L(t,a) \quad \begin{matrix} L(t,0) = g_L(t) \\ L(0,a) = a_L(a) \end{matrix} \quad (2)$$

$$\frac{\partial St}{\partial t} + \frac{\partial St}{\partial a} = -\mu_{St}(\cdot)St(t,a) \quad \begin{matrix} St(t,0) = g_S(t) \\ St(0,a) = a_S(a) \end{matrix} \quad (3)$$

$$\frac{\partial R_t}{\partial t} + \frac{\partial R_t}{\partial a} = - \mu_{R_t}(\cdot) R_t(t,a) \quad \begin{aligned} R_t(t,0) &= g_R(t) \\ R_t(0,a) &= a_R(a) \end{aligned} \quad (4)$$

$$\frac{\partial F}{\partial t} + \frac{\partial F}{\partial a} = - \mu_F(\cdot) F(t,a) \quad \begin{aligned} F(t,0) &= \beta_F(t) \\ F(0,a) &= \gamma_F(a) \end{aligned} \quad (5)$$

$$\frac{\partial M}{\partial t} + \frac{\partial M}{\partial a} = - \mu_M(\cdot) M(t,a) \quad \begin{aligned} M(t,0) &= g_M(t) \\ M(0,a) &= a_M(a) \end{aligned} \quad (6)$$

where the independent variable t and a are time and age respectively measured in day-degrees (D°). Note that in simplest deterministic form $dt = da$. In fact, $dt \neq da$ in nature because individuals in the population tend to age at different rates. Various methods have been developed to model this dispersion of ages (see biophysical models section). $L(t,a)$, $S_t(t,a)$, $R_t(t,a)$ and $M(t,a)$ are mass density functions for leaf, stem, root and fruit tissues respectively, while $\rho(t,a)$ and $F(t,a)$ are number density functions for whole plants and fruit. The term I (eqn. 1) is a net immigration rate (in a general sense, it could be new seeds or other plant propagation methods). This term is not applicable to domestic cotton crops, but is important for wild cotton where new seed may be blown into the area encompassing the study population. It is included in equation 1 to make the model general for any population of plants. The various $\mu(\cdot)$ are again complex age-specific death rates. The fruit model could be written as (Wang et al., In Press)

$$\frac{\partial F}{\partial t} + \frac{\partial F}{\partial a} + \frac{\partial (g_m)F}{\partial m} = - \mu_F(\cdot) F(t,a,m) \quad (7)$$

Only the nutrient pool submodel differs in form. Let $C(t)$ be the carbohydrate material present in the pool at time t , then C satisfies the following equation

$$\frac{dC}{dt} = \frac{dP}{dt} - \left(\sum_{i=1}^3 \theta_i(t) + \dot{L} + \dot{R}_t + \dot{S} + \dot{M} \right) \quad (8)$$

where dC/dt is approximated by $(-C(t) + C(t+\Delta t))/\Delta t$. The differences representation of equation (8) is then

$$C(t+\Delta t) = C(t) + \frac{dP}{dt} \cdot \Delta t - \left(\sum_{i=1}^3 \theta_i(t) + (\dot{L} + \dot{S}_t + \dot{R}_t + \dot{M}) \right) \cdot \Delta t \quad (9)$$

The θ_i are various metabolic costs associated with maintenance respiration, production photosynthate (ΔP) and maintenance respiration of all living tissues (see Hesketh et al. 1971). \dot{L} , \dot{S}_t , \dot{R}_t , and \dot{M} are maximum potential growth rates for these plant tissues, and are greatly modified by temperature, plant crowding and various other factors. In equation (9)

$C(t) + \frac{dP}{dt} \cdot \Delta t = \text{the supply}(Q)$, while $\left(\sum_{i=1}^3 \theta_i(t) + (\dot{L} + \dot{S}_t + \dot{R}_t + \dot{M}) \right) \cdot \Delta t = \text{the demand}(D)$.

If $r = Q/D < 1$, then the following occurs: (1) The production of new fruiting points and mainstem nodes slows as a function of r , (2) a priority scheme for allocating the photosynthate occurs (Gutierrez et al. 1975). Fig. 1a depicts the population model and its intimate association with the metabolic pool, while 1b depicts the metabolic or carbohydrate pool model. In cotton, the priority scheme works as follows.

- 1) Metabolic costs associated with maintenance and photosynthate production are used first.
- 2) Respiration costs associated with fruit growth and some or all of the maximum fruit growth occurs.
- 3) If any photosynthate remains, some of the leaf, root and stem growth occurs as described above.

This model for carbohydrate allocation has been used to successfully model several Acala cotton crops in the San Joaquin Valley of California, a 1975 DP-16 cotton crop in Phoenix and a Nicaraguan

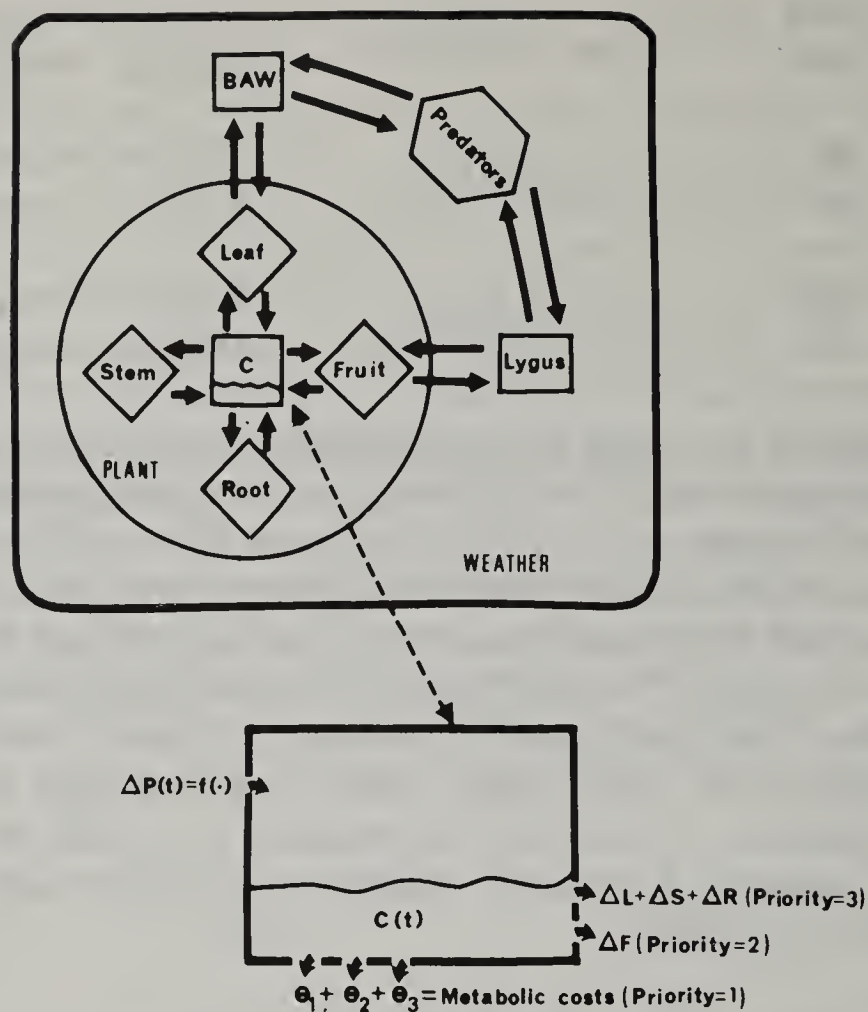


Fig. 1. –The interaction of plant growth and development – two herbivores (BAW – beet armyworm and Lygus bug) – their natural enemies and weather (A). The carbohydrate pool submodel is shown in greater detail (c.f. Gutierrez et al. 1975, and Wang et al., In Press) (B).

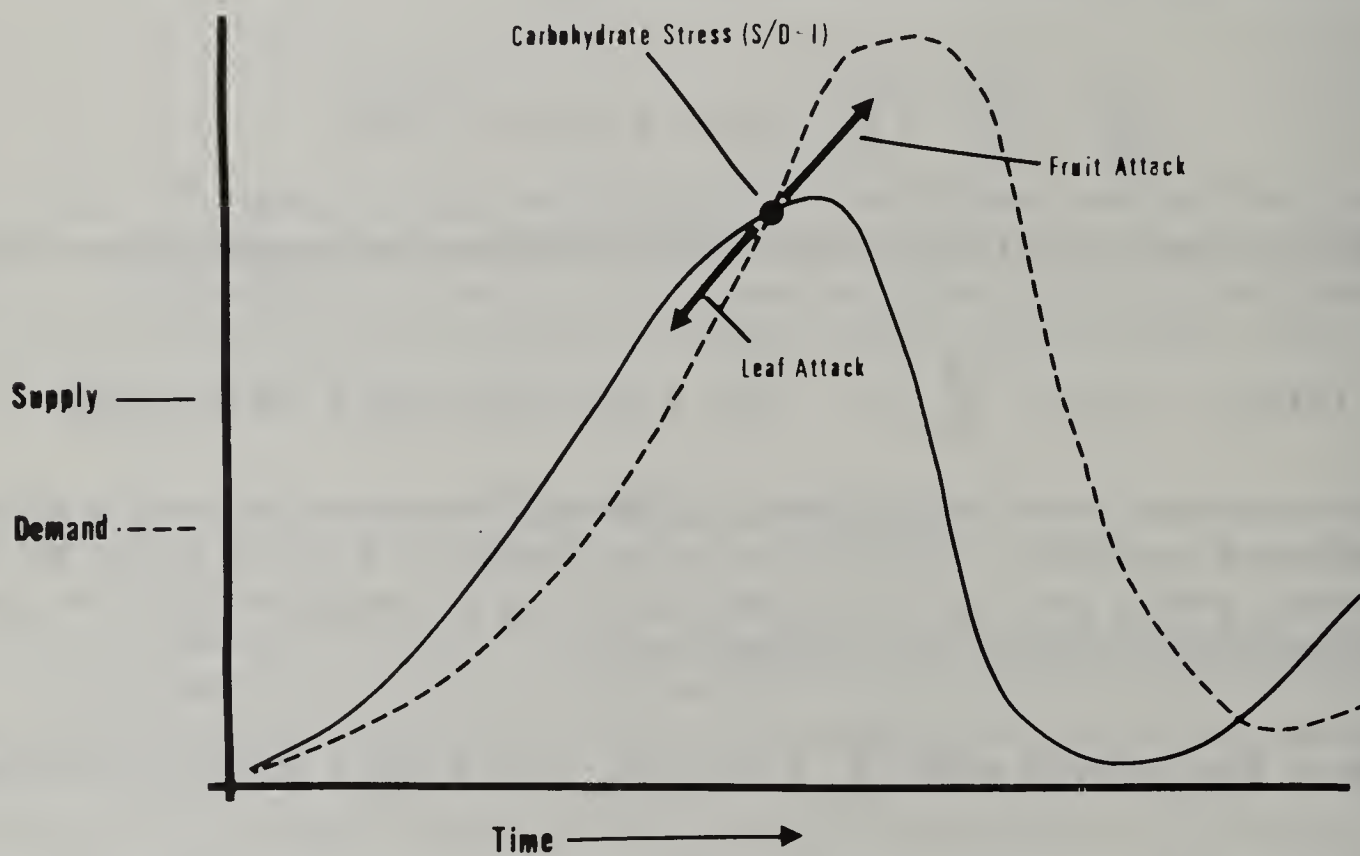


Fig. 2. –The trends in carbohydrate demand by cotton plants, as well as the effect of leaf and fruit feeding insects on the timing of carbohydrate stress in the plant population. Note that $s = \text{supply}$ in this figure.

variety. The model is very general in form, and merely requires that variety specific estimates for \dot{L} , \dot{S} , \dot{R} , \dot{M} and fruit production time delays be incorporated.

Figure 2 (c.f. Wang et al., In Press) shows us how the plants respond to insect damage. If the herbivore attacks leaves, it affects $dP/dt \cdot \Delta t$ directly and by diverting C to wound healing. If the fruit are attacked, it reduces the demand all causes the materials to be diverted to vegetative parts (L , S , R). In the latter case, plants grown closely together may start to shade each other, such that the $\Sigma \theta_i$ may increase relative to $dP/dt \cdot \Delta t$ such that the plants may become unthrifty. This is commonly observed when large numbers of *L. hesperus* attack cotton early in the season (Gutierrez, Leigh et al., In Press).

The insect models – The model for any particular pest (N_i) species is very similar in form to that for the individual plant part components

$$\frac{\partial N_i}{\partial t} + \frac{\partial N_i}{\partial a} = - \mu_i(\cdot) N_i(t,a) + I_i \quad (10)$$

Similar supply/demand ratios are operative. If the food requirement for the population are not met, the rate of increase is slowed. It could be that oviposition sites or other essential requisities may also be limiting. Models of this type have been published by Gilbert and Hughes (1968), Gilbert and Gutierrez (1973) Gutierrez et al. (1974a, b), Barr (1974). Only Gutierrez et al. (In Press a, b) and Y. Wang et al. (unpubl.) have successfully coupled plant-herbivore-weather interactions in this manner. Similar methods (i.e., supply/demand) also apply to predator-herbivore interactions.

Bio-physical models

Accuracy and further advancement of population modelling requires that relevant stochastic processes (e.g., Barr 1974) and appropriate behaviour be included (Jones, R. In Press), and that the underlying physiological processes affecting age specific survivorship ($1x(\cdot)$) and natality ($Mx(\cdot)$) be described in rigorous mathematical terms. Considerable progress has been made in this area.

The basic premise in much of the work is that survival and developmental rates, and most other factors or plant and insect population dynamics are controlled by the thermal environment. For example, much of the earlier work on developmental rates of insects and plants used the notion of day degrees. This concept assumes that their developmental rates are exactly proportional to temperature throughout much of the range favorable to their environment (Fig. 3, section b) (see Campbell et al. (1975) for a recent review). In fact, many studies have shown that this is not the case, and the extremes of the rate of development curve shown in Fig. 3 depicts these departures from the linear model (c.f. Stinner et al., 1974). Sharpe and DeMichele (In Press) developed a stochastic thermodynamic model for the development of poikilotherm organisms. The model is derived from the Eyring equation which assumes multiple activity states of the underlying developmental control enzymes. This model describes the entire relationship from a more theoretical and scientific base, and in addition, contributes to scientific understanding. As a result, the model allows for more accurate prediction of population phenology and aging. An extension of this model by P.J. Sharpe et al. (unpubl.) shows that the skew in the distribution in developmental times observed by Stinner et al.

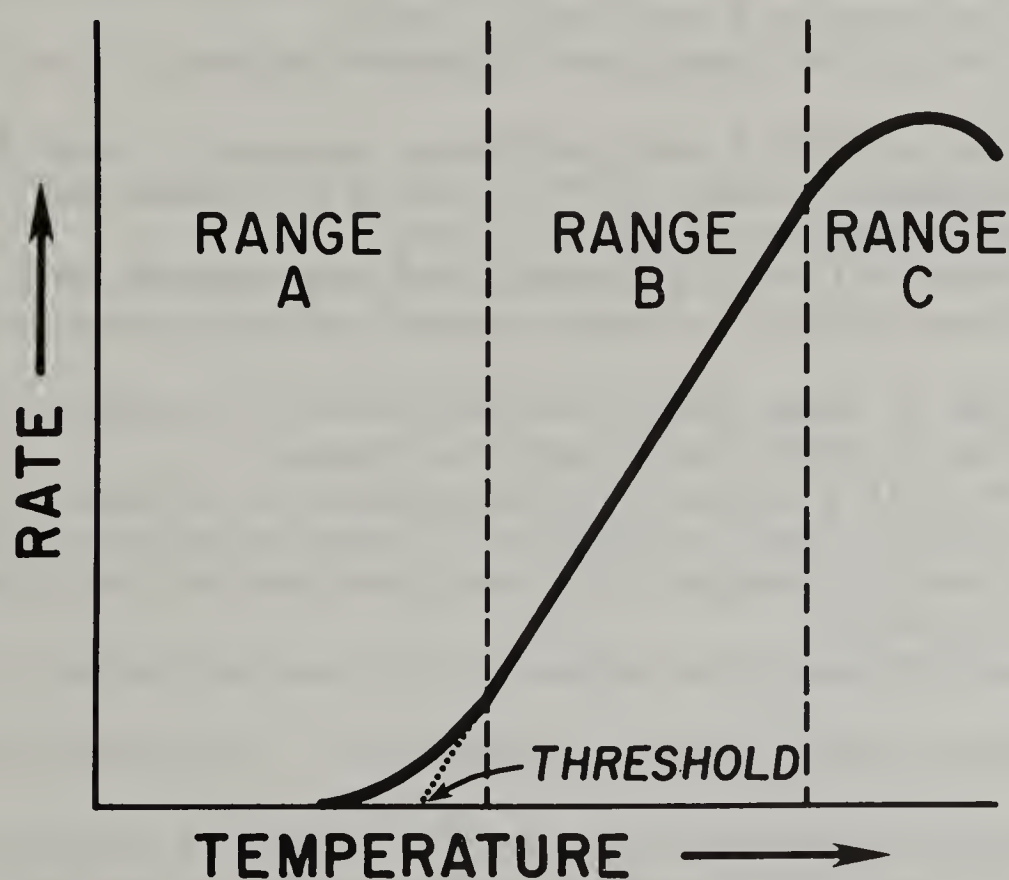


Fig. 3. –The relationship between the rate of development of poikilotherm organisms and temperature. The estimated thermal threshold is based upon a linear model. The departure from a linear model at A is caused by low temperatures, while that in region C is caused by lethal high temperatures.

(1975) and others, results naturally from the transformation from developmental rates to emergence times. The underlying assumption is that the concentration of enzymes which are rate controlling for development are symmetrically distributed about some genetically determined mean concentration. These two simple, yet elegant, biophysical models are used to describe not only the rate of development of a population, but also the distributions of their developmental times. Both of these models are easily incorporated in the population models developed above.

Other models of this type seek to estimate the amount of thermal energy which penetrates a plant canopy, J.E. Mann et al. (unpubl.). This information is of special importance to both the plants (say cotton) and some of its pests (e.g., boll weevil). In the first case, light penetration greatly influences photosynthate production while in the latter case, too much light (heat) causes up to 90% mortality in boll weevil larvae developing in cotton squares which have fallen to the ground. DeMichele et al. (In Press) developed a theoretical model to predict the drying of cotton squares as influenced by light penetration, while G.L. Curry et al. (unpubl.) extended this model to simulate the effects on immature boll weevil survival. Their results were in very good agreement with experimental work conducted by Isely (1932), but must now be extended to field conditions.

Field application of models — We stressed above that models should not be used principally as predictive tools because in the foreseeable future not all of the components can adequately be modelled in a rigorous fashion. Furthermore, it is impossible to predict weather, hence only very short term predictions are possible. For some purposes, this may be adequate (i.e., the phenology of some pest), but for total ecosystem prediction, it seems at present highly unproductive.

Models can be used to develop strategies for ecosystem management (e.g., Regev et al., 1976), or to ascertain more precisely the pest status of some species (e.g., *Lygus hesperus* in California cotton). Predicting farmer yields with our current tools is sheer folly, and should be discouraged. However, the development of realistic ecosystem models to enhance our understanding of dynamic processes is indeed very worthwhile, and should be encouraged.

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The Ecological Basis of Biological Control

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Introduction

Classical biological control has been a widely used means of controlling exotic pests (DeBach 1964; Huffaker and Messenger 1976). Its status as a discipline can be traced to the dramatic success achieved with the vedalia beetle, *Rodolia cardinalis* (Mulsant), when it was introduced against the cottony cushion scale, *Icerya purchasi* Maskell, in California during the late 1880's (Doutt 1964). This success stemmed from the attempted introduction of as many of the natural enemies as were found associated with the scale in its native home — Australia. The only factor which limited a natural enemy's being introduced was its inability to survive the long sea voyage to California. This initial approach typified much of the early work in biological control and it is from such attempts that the impression is often gained that biological control strictly employs trial and error methodology.

This impression, however, is certainly in error even for the cottony cushion scale project because that effort itself had a theoretical basis. It had long been observed that many of the pests of early American agriculture were alien and most of them were of little or no consequence in their homelands (Doutt 1964). A number of early entomologists theorized that these problems might be redressed by introducing their natural enemies. The cottony cushion scale, and other examples following it, provide ample evidence supporting this general theory. Some 186 partially to fully successful examples of biological control of pest species exist involving some 384 partially to fully successful projects. (Laing and Hamai 1976). This which is substantial testament to the relevance of this premise.

As recently expressed by Messenger (1976), "The fundamental concept underlying biological control is that of natural control of population numbers, often described by the term 'balance of nature'. Other theoretical concepts of general significance to ecology as well as biological control that are subsumed by this concept of natural control include the density dependent competition for resources among the members of the same population and species, the reciprocally density dependent regulation of both host and parasitoid [or prey and predator] numbers by the exploiter species [natural enemies], competition between different species, and the specificity and [degree of] stability of the various trophic relationships among the organisms in a community."

Natural control is the combined process by which populations are limited in nature and, while it includes at least one density dependent component, any factor which affects mortality, natality or dispersal is a part of this process. It is the complex interaction of these various factors which leads to the characteristic densities we observe in nature (see Huffaker and Messenger 1964, and Huffaker et al. 1971).

This paper, then, is an effort to review those theoretical concepts and principles of ecological relevance to biological control. We will first discuss the attributes of an effective natural enemy as

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biologically and empirically established, then a number of models which embody certain of these concepts and attributes in order to obtain more explicit insights into these properties. Finally, we suggest procedures and criteria by which better programs might be planned, appropriate natural enemies selected (parasites, predators and pathogens) and habitats manipulated to conserve and augment those natural enemies already present, both native and introduced. It is hoped that from this treatment the necessary dependence of biological control on ecological theory is more clearly established.

Attributes of an Effective Natural Enemy

The principal attributes of an effective natural enemy may be categorized as follows: (1) fitness and adaptability, (2) searching capacity, (3) power of increase relative to the host (prey), (4) host specificity and host preference, (5) synchronization with the host and its habitat, (6) density-dependent performance relative to either or both the host's density (including aggregation) and its own density (including mutual interference), (7) detection and responsiveness to the condition of the host, and (8) competitive ability. This list is predicated on traditional as well as more recent concepts and on whether or not useful criteria can be developed for judging potentially valuable natural enemies. Further on, it will be seen that these criteria are not mutually exclusive: the notions involved in one category often imply those of another (see e.g. DeBach and Doutt 1964, Huffaker et al. 1971).

1. *Fitness and Adaptability*

This attribute is so all-inclusive and so generally recognized that it will not be discussed separately. Messenger and van den Bosch (1971) deal with its various aspects in some detail. These aspects are inherent to most, if not all, of the separate attributes dealt with below, and are referred to when appropriate.

2. *Searching Capacity*

Most biological control specialists consider searching capacity as the single most important attribute of an efficient natural enemy. It has generally been conceived as that set of properties which permits a host specific parasite species to maintain itself at low host densities. When a more formal definition has been attempted, it has proven unsatisfactory. The concept is normally defined in terms of a parasite's ability to find hosts during its lifetime. Thus, all other things being equal, the parasite species with the shorter life expectancy in the environment would have the lower searching capacity. It is this notion which Nicholson (1933) used for his "area traversed"; that is, the total areal tract "censused" in searching by an average parasite (of a given species) during its lifetime. Thus searching capacity in this sense is a constant for a given parasite strain under specified environmental conditions. Therefore, a species' fitness and adaptability under varying conditions are inherent to its lifetime searching capacity.

Unfortunately, the original concept has become confused with that for the "area of discovery" of Nicholson (1933) and Nicholson and Bailey (1935). Although Nicholson and Bailey derived the idea from the "area traversed", they defined the "area of discovery" for an average parasite as the ratio of the number of unparasitized hosts to the total number initially present $a = \frac{1}{p} \log_e \frac{N}{S}$. (See

Section III-6 for further discussion). In their view, the "area of discovery" was also a constant; thus, there is an assumed relationship between this concept and the notion of searching capacity. But, as has been pointed out by a number of investigators, the "area of discovery" is not constant but commonly varies with density changes in both host (Holling 1966, Royama 1971, Huffaker and Matsumoto in press) and parasite populations (Hassell and Huffaker 1969, Hassell and Varley 1969, and others).

It now seems obvious that the concept of searching capacity has become ambiguous in any formal sense. We cannot explicitly specify those properties which make an entomophagous species an efficient searcher. However, we do have concepts concerning properties which permit it to search well and maintain itself at low host densities. Doutt (1964) referred to these concepts as rather

elusive factors, e.g. power of locomotion (dispersal to a habitat and host searching in the habitat), power of survival, and aggressiveness and persistence.

3. Power of Increase

As has previously been mentioned, searching capacity has been thought to be more important than the power of increase. This stems, historically, from the emphasis placed on the biological control of pests in perennial crops, especially fruit tree crops having comparative continuity in space and time. Thus, high rates of increase were thought to be relatively less important once the natural enemy achieved regulation of its host (at equilibrium). In the hypothetical steady state it would only need a power of increase sufficient for replacement of the parent population — one female progeny per female parent.

However, a true steady state does not occur, and especially in frequently disturbed habitats such as those involving row crop agriculture or frequent pesticide applications. Under these more disturbed circumstances a high power of increase is a very desirable attribute, especially if the natural enemy is to be used for inoculative releases in which the objective is pest suppression during the immediate crop season. Moreover, in row crops rather generalized predators may be more important than highly host specific parasites (Ehler et al. 1973, Newsom 1976). Thus a high power of increase is an important criterion for selecting natural enemies when they are to be used in frequently disturbed or discontinuous habitats or where they cannot survive the winter.

Of major importance, it is a common error to consider that a natural enemy having a lower reproductive power than its host would be unable to overtake or suppress its host populations. One of us (Messenger 1976) neglected to consider the amount of host mortality caused by the parasite he presented a graph of the influence of temperature on the intrinsic rate of increase of three species of parasites of the aphid *Therioaphis trifolii* Buckston. The shaded areas were interpreted to represent the range of conditions capacity to control the host. Actually, a natural enemy need only possess an intrinsic power of increase sufficient to offset that part of the intrinsic power of increase of the host that is *not* negated by the host mortality caused by the natural enemy (Huffaker and Messenger (1964, p. 107), Huffaker and Flaherty (1966), Huffaker et al. (1970)). Models of interaction automatically incorporate this feature.

One way to ascertain the effective reproductive increase and numerical response potential in the field would be to add, say, three or four effect of density categories of the host to a natural habitat where the host and parasite densities are very low (and adult female parasite densities can be ascertained). The rate of increase in density of females, generation to generation, would furnish an estimate of the numerical response potential (Fig. 1).

This test would combine searching effectiveness in its various components (Sections II & III) with reproductive capacity, and the results, if replicated in time and place, would reveal the parasite's capacity to respond to increases in host density due to reproduction in the field, the major factor of importance in maintaining control at low host density.

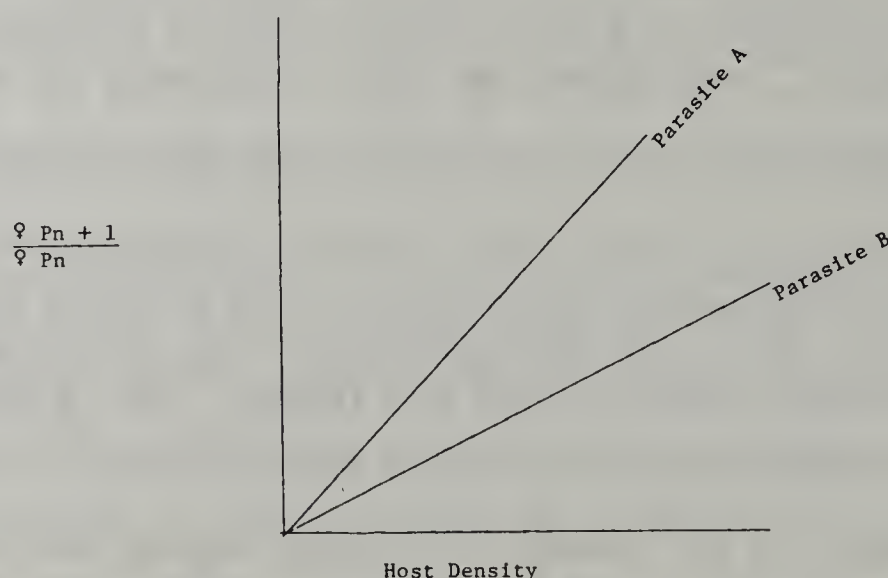


Fig. 1.—Numerical response capability of two parasite species (A) and (B) relative to initial host density: φP_n = number of female parasites in the parent generation, φP_{n+1} = number in the progeny generation.

4. Host Specificity and Host Preference

Classical biological control has favored introduction of highly host-specific natural enemies. Doutt and DeBach (1964) have noted, "At least, most successes have resulted from the introduction of rather host-specific entomophagous species". Clausen (1958) stated, "In the history of biological control instances of successful utilization of parasites from another host genus are exceedingly rare". It would seem that experience has supported this premise.

But there is also an additional reason for this view. A host-specific parasite is one which has coevolved with its host; thus, it is likely to be more attuned to its host's biochemistry, behavior, habitat preferences and phenology than one less intimately associated. Lacking host-specificity, the ability of a natural enemy to develop high host or prey preference for the target insect in the given situation is highly desirable (Zwölfer et al. 1976; Simmonds 1969; Huettal and Bush 1972). Thus, host-specificity has proved to be, from a practical point of view, a useful criterion by which to select candidate natural enemies for introductions, although it needs to be judged somewhat differently according to the objectives to be met. Such a co-evolved association also suggests the parasite species might well exhibit a more reliable and regulating, reciprocal density-dependent interaction with its host in stable situations. Non host-specific natural enemies may be very effective suppressive agents and some may possess considerable true regulative capacity by virtue of switching their prey preferences (See Section III).

5. Synchronization

An effective natural enemy must be behaviorally and reproductively synchronized with the developmental phenology of its host as well as the seasonal phenology of its host's habitat. Synchrony of this sort is most likely to be found with a highly host-specific parasite. Some introductions appear to have failed because the natural enemy lacked synchrony with its host. Clausen (1956), Messenger (1971), and van den Bosch and Messenger (1973) cite examples. Synchronization is of course a form of fitness and adaptability. There have been relatively more biological control successes in warm or at least mild, salubrious environments. The more rigorous climatic environments seem to make effective and reliable natural regulation less likely, Doutt and DeBach (1964) think, for two reasons: (1) because of excessive direct mortality of the natural enemies, and (2) because of the more precise requirement in synchronization of natural enemy voltinism or diapause. The pest insects of salubrious areas lack an obligatory diapause and they pose fewer problems of synchronization for a natural enemy. Yet, the number of successes in Canada, northern United States, Tasmania and New Zealand attest to the fact that the necessary adaptations, including synchronization to rigorous conditions, are often met. Thus, synchrony is also a criterion of value in judging the potential of an entomophagous species.

6. Density-Dependent Performance

A truly host-specific natural enemy is clearly dependent on its host for its existence. A favorable environment, a high searching capacity and even moderate powers of increase would likely make it capable of regulating the density of its host. There are several aspects to this coupled, reciprocal density-dependent interaction; namely, (1) the functional response; (2) the numerical response and (3) their modification by environmental conditions such as temporal and spatial heterogeneity, mutual interference and extrinsic damping factors (See details, Section III). In considering mortality only (since we are discussing the effects of a biological control agent) a density-dependent response exists when the natural enemy's net response causes an increasing percentage kill with increasing host density and a decreasing percentage kill with decreasing host density.

If an *individual* parasite finds and successfully attacks *proportionately* more hosts with increasing host density (within a low range of host densities) the numbers killed follow an s-shaped curve. This type of functional response, if strong enough, will lead to population regulation, i.e. it will provide stability (Holling 1965, Hassell and May 1973, Murdoch and Oaten 1975). However, most entomophagous species studied exhibit a functional response of the type described by Holling's (1959b) "disc equation". This type of response itself results in a decreasing percentage kill with increasing host density (no controlling potential). However, such a natural enemy might still regulate

the density of its host through its numerical response if it has several generations to one of its host. But if the parasite has a single generation to one of its host then its reproductive response is delayed density-dependent (Varley 1947). This condition poses some theoretical problems in modeling host parasite interactions but nevertheless empirical evidence clearly documents the fact that parasites exhibiting delayed density-dependence can control and regulate the densities of their hosts (See further Section III).

Moreover, it seems reasonable that such a natural enemy would acquire through natural selection the property of aggregating to some extent in spots of greater host (prey) density and when they themselves become overly crowded that they would exhibit some form of intraspecific competition (mutual interference).

Thus, the general belief seems reasonable that rather highly host-specific natural enemies having high *field* searching capacities are most likely to exhibit a net regulating density-dependent response to changes in host density. Thus, using these two criteria as the principal ones for choosing a candidate natural enemy for classical biological control in rather stable habitats will likely ensure the presence of an adequate density-dependent response.

7. *Detection of, and Responsiveness to the Condition of the Host*

A natural enemy may have an excellent inherent searching capacity and yet waste much of that potential by failure to detect previously parasitized hosts or the precise stage of the host suitable to it, or in addition, it may fail to exercise restraint in oviposition, or its discrimination may be broken down, resulting in wasted time and energy, and sometimes in enormous waste of progeny. *Aphytis maculicornis* Masi, is a superb biological control agent of olive parlatoria scale, *Parlatoria oleae* (Colvee), in a physically favorable environment, partly because of its precision in host species and host stage perception, discrimination and restraint (Huffaker and Kennett 1966). Doult et al. (1976) give an account of the remarkable perfection often reached in adult parasitoids in terms of finding, accepting and utilizing their hosts.

8. *Competitive Ability*

High competitiveness is not of itself a requirement for biological control. Pragmatically, it does not matter whether economic control is achieved with a single, highly efficient natural enemy which displaces all others or from a combination of species that coexist and together accomplish the same degree of control. Messenger (1976) lists a few examples of each type of biological control, but DeBach (1964, 1974) stated that most successful examples of classical biological control result from the introduction of a single highly efficient natural enemy.

Competition between parasite species can be classed as *intrinsic* if occurring within or on the host, or *extrinsic* if exterior to the host. Intrinsically superior competitors will succeed over intrinsically inferior ones when they compete in or on the same host as immature individuals. Consequently, for an intrinsically inferior species to persist, it must be competitively superior extrinsically. Such a requirement implies a high searching capacity which again is considered the most important requirement of an effective natural enemy. For this reason Franz (1961) suggested that parasites should be introduced in a sequence starting with the apparently most promising intrinsically inferior ones and introducing intrinsically superior ones only if the first ones fail.

It has been stated as a principle that multiple introductions will jeopardize biological control through the results of competition, including that by intrinsically superior parasites (Turnbull and Chant 1961, Turnbull 1967).

Examples are known in which the effectiveness of host-specific parasites were reduced because of age class discontinuities in the host population caused by the introduction of a disease (Ulyett 1947) or general predator (Taylor 1937). Furthermore some workers (e.g., Pschorn-Walcher et al. 1969; Zwölfer et al. 1976) have suggested that the presence of a complex of parasitic species has produced a "balanced" check on the combined control of the host population achieved by the complex. Using models, Hassell and Varley (1969) and Varley et al. (1974) found little support for these views (see Section III.7) but they only considered host specific parasites.

Regarding multiple introductions, Hassell and Varley (1969) stated, "As long as hyperparasites and non-specific parasites are excluded, there is little danger from successive [multiple] introduction,

and the more species which can be established, the lower the pest density is likely to become." Varley et al. (1974), state relative to Turnbull and Chant's (1961) and Turnbull's (1967) warnings: "Their view is supported neither on theoretical grounds [modeling] nor by practical experience." Varley (1947) had originally suggested the possibility that introduction of a complex of specific natural enemies might reduce overall control compared to that which the "best" one (at a given place) could achieve alone, but he did not formulate it as a fixed position but one requiring examination.

Competitive displacement of established parasites by newly introduced ones has been commonplace in classical biological control. A recent survey of biological control (Huffaker and Messenger, eds. 1976) identified numerous examples of competitively displaced species, all of which appeared to result in improved biological control. (See also DeBach 1966, and Huffaker and Kennett 1969).

A hyperparasite can sometimes act as both a primary and secondary parasite, functioning either as a direct competitor or natural enemy of the primary species. While theory suggests that hyperparasitism may under certain conditions act as a stabilizing factor (Luck and Messenger 1976), far too little is known about these conditions to justify the introduction of hyperparasites for this purpose. Further, the existence of such a stabilizing function has yet to be documented empirically or observationally.

A serious threat to established biological control exists from the intrinsically superior parasites which act as cleoptoparasites (parasites which prefer hosts already attacked by a primary species) (Arthur 1964). Thus, these species are, in the practical sense, equivalent to hyperparasites and should be excluded.

Additionally, a great deal of care should be exercised in introducing rather general parasites or predators since they might eliminate host-specific ones by their sheer numbers when the former are temporarily more abundant than the latter because of dense populations of an alternative host(s) (or, as above, they can disrupt availability of the proper age-class of the host).

9. *Summary of Attributes*

In summary, those attributes which describe an efficient self-sufficient natural enemy are high searching capacity, a good degree of host-specificity, sufficient power of increase to overtake and suppress the host population, synchrony with the host and its habitat, and a density-dependent response to changes in and their own density host density when that species exists. In general, these qualities are most likely to be possessed in a natural enemy able to maintain itself in the field on a single host species at low host densities. Thus, this working definition of good searching capacity becomes an extremely useful criterion for judging potential candidates for introduction. How does this affect the need to improve upon our largely empirical understanding of the host-parasite/predator-prey interaction? It is to this point we now turn.

Theoretical Models and Biological Control

The models we discuss are deterministic ones which describe a predator-prey or host-parasite interaction and whose parameters are well-defined constants. They can best be characterized as abstractions aimed at illuminating general principles involved in such relationships, as contrasted to a model of an empirical nature whose purpose is a description of a more real life system with some practical purpose in mind. General insights into the dynamics of abstract population models are gained by stability analysis. The mechanics of mathematically analyzing stability can be found in May (1973), Smith (1974) or Murdoch and Oaten (1975) and, therefore, will not be presented here. We are interested especially in synthesizing the results of such analyses as they apply to biological control.

It is essential first, however, to define what is meant by "stability." Here we follow the notions of May (1973) and Smith (1974). In a stability analysis we wish to determine what happens to the populations if they are slightly perturbed from their equilibrium state. If they return to their equilibrium they are stable, if they continue to increase or to decrease, or oscillate at increasing amplitudes they are unstable. These two conditions are separated by one of neutral stability, a condition in which the population densities either remain at the perturbed level or exhibit oscillations

of constant amplitude. In the latter case the amplitude of these oscillations is determined by the magnitude of the initial displacement. These ideas are represented schematically in Figure 2.

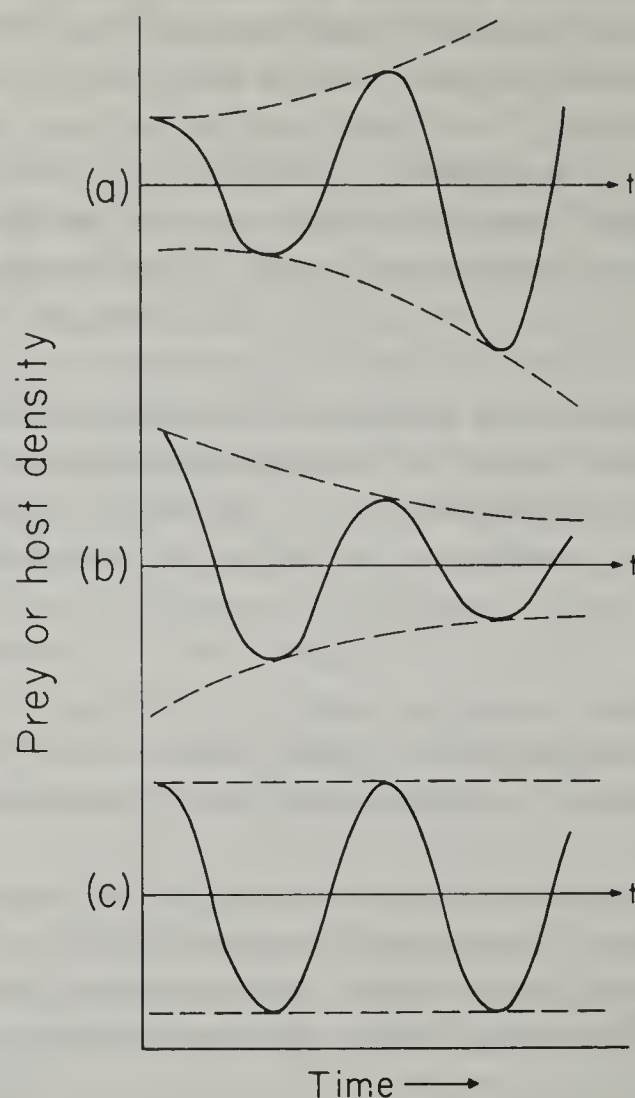


Fig. 2.—Schematic illustration of a deterministic system which when perturbed from equilibrium is (a) unstable, (b) stable, and (c) neutrally stable. (After May 1973)

To analyze these models for stability we investigate their population trends within the vicinity of their equilibrium points, i.e., we characterize their neighborhood stability. Since population models are non-linear their global stability cannot usually be investigated. Perhaps it is easiest to think of these notions with reference to geometric landscapes. If we compare a convex surface with a concave one, then the convex surface is unstable. Although we might be able to balance, say, a marble at the peak of such a convex surface, any perturbation will cause it to roll away from its equilibrium point. Any perturbation of a marble within a concave surface results in its return to its equilibrium point, the “bottom.” However, even if a model is found to be stable by this analysis we are unable to determine, by analogy, whether the marble lies within a concave recess in a convex mountain bulge or within one representing a very large valley considered alone. In the case of the former, too large a perturbation causes the marble to move beyond the edge of the recess and fall down slope “seeking” some new stability point; while in the latter case, the same large perturbation results in the marble’s return to the valley bottom.

In addition to the mathematical method of analysis, a graphical one also exists. Calculating the population densities for predator-prey or parasite-host populations at each generation during an interaction, plotting these densities on a graph, one against the other, and joining the points sequentially indicates whether the model is stable for the specific parameter values, based upon the criteria provided in Fig. 3. This process must be repeated using different values for the parameters if one wishes to determine under which conditions (parameter values) stability exists. Determining a model’s stability using traditional mathematical (analytical) methods is less time consuming and therefore more desirable when this approach is possible. (A more general graphical analysis also exists — see Section III-3).

Lastly, a non-linear population model need not be characterized by a point equilibrium; rather, it may be characterized by a stable limit cycle, i.e., the population densities change in a cyclic pattern. Such interactions differ from those exhibiting neutral stability. In the case of the former, the populations return to those densities which characterized their stable limit cycle before perturbation; in the latter case, the densities will continue to oscillate at an amplitude determined by the magnitude

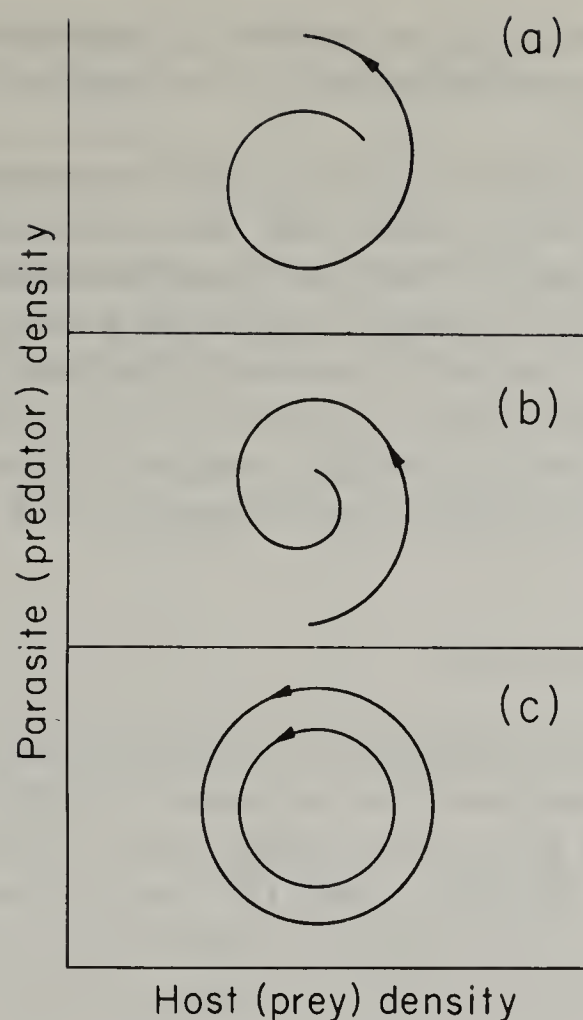


Fig. 3.—Predator-prey (host-parasite) population graphs of sequences of population density suggesting (a) unstable, increasing amplitude, (b) stable, (c) neutrally stable interaction.

of the initial displacement. However, without an analysis of an interaction exhibiting oscillations, the type of stability implicit in the interaction cannot be determined.

Thus, we can have stable point equilibriums, unstable point equilibriums, stable limit cycles and neutral stability as population interaction responses, as represented by host-parasite or predator-prey models. In the following discussion we are interested in the types of predator-prey/host-parasite interactions which lead to stability, the type of stability which results, and their implications for biological control.

The Models

1. The logistic growth model

Perhaps the earliest model of relevance to biological control is Verhulst's logistic equation [eq. 1] (Verhulst 1838, Pearl and Read 1920). This model combines two general concepts: the propensity for populations to grow exponentially and the resistance of the environment to such growth. The interaction of the two processes leads to a "leveling off" of population size at a characteristic density often referred to as the environment's carrying capacity — implying, thus, a density dependent process. This is accomplished in the model by incorporating a direct density-dependent interaction, the intensity of which is governed by the difference between the population density (N) at time t and that sustainable by the environment (K), the smaller this difference the more intense is the environmental resistance.

The model is commonly written

$$\frac{dN}{dt} = rN \left(\frac{K-N}{K} \right) \quad (1)$$

where r is the intrinsic growth rate under a specified set of environmental conditions, N is the population density at time t and K is the carrying capacity of the environment (maximum population density which the environment can sustain). The model is based on a number of simplifying assumptions: (1) the population's density can be represented by a single variable, N (ignoring such population heterogeneity as age structure, sex, genotype or spatial distribution); (2) the effects of

deaths and births are instantaneously felt throughout; (3) changes in density are deterministic (implying that these changes (dt) are unambiguously known and can be determined solely from the conditions (states) present at time t).

Any effect from natural enemies would be incorporated as environmental resistance, i.e., within the $(K-N/K)$ term of eq. 1. In fact, Smith (1935) used the concept embodied in this model to argue that host (prey) populations were indeed limited by their natural enemies but he never formulated his concepts or arguments mathematically. Clearly, this model is not a description of a two species host-parasite or predator-prey interaction and is thus only of indirect interest to biological control. It is historically, however, the first model which recognized that populations are limited in the densities they can reach. May (1973) presented the stability analysis for this model, showing the familiar result, i.e., the model has two stable equilibrium points, one at $N = K$, if and only if $r > 0$; and one at $N = 0$, if and only if $r < 0$.

2. Lotka-Volterra predator-prey model

Lotka (1925) and Volterra (1926) independently developed the first models specifically dealing with two species predator-prey interactions. They conceived, (1) that the rate of change of the prey population (dN_1/dt) is a function of its intrinsic growth rate (r) and the rate at which the predators are removed from the population ($\gamma_1 N_1 N_2$); and (2) that the rate of change of the predator population (dN_2/dt) is a function of the predator's death rate in the absence of prey ($-d$) and the growth rate of the predator population per unit of prey consumed (γ_2). Thus,

$$\frac{dN_1}{dt} = rN_1 - \gamma_1 N_1 N_2 \quad (2a)$$

$$\text{and } \frac{dN_2}{dt} = -dN_2 + \gamma_2 N_1 N_2 \quad (2b)$$

where N_1 and N_2 are the predator and prey population densities respectively, r the intrinsic growth rate of the prey population, $-d$ the intrinsic death rate of the predator population, γ_1 the proportion of contacts between predator and prey which prove fatal to the prey, and γ_2 the efficiency of the predator in converting consumed prey into offspring.

This model is, of course, based on a number of assumptions in addition to those made for the logistic equation: (1) in the absence of predation, the prey population increases exponentially and without limit; (2) the predator's rate of death ($-d$) is assumed to be constant and thus independent of predator or prey density; (3) the efficiency of converting consumed prey to predator offspring is also assumed to be constant and independent of predator or prey density; (4) the proportion of prey killed by the predator is constant and therefore simply the product of the contacts between prey and predator individuals; (5) the movements and contacts between predators and prey are assumed to be random; (6) the time involved in the prey's consumption is negligible (Smith 1974).

Analysis of the model shows it to be neutrally stable. The oscillations fail to either grow or dampen when the predator and prey population densities are perturbed. This implies that the predator population lacks the ability to regulate the prey's density, at any specific level. Making the model more complex by increasing the number of predatory and prey species, i.e., making it a multiple-species model, wherein a predator can feed on any of the predator species, does not improve the model's stability (May 1973). In fact, the model may become less stable and therefore purge itself of species until a condition of neutral stability is reached. This would suggest that species diversity per se does not necessarily lead to stability. Beyond this conclusion, however, the Lotka Volterra model provides little insight into the predator-prey interaction which might help explain field observations involving biological control or provide criteria by which effective biological control agents might be judged. Its assumptions are too unrealistic. Its use, however, is instructional.

3. Modifications to the Lotka-Volterra Model

Rather than cataloguing and discussing the modifications to the Lotka-Volterra model which are present in the literature (see May 1973, Smith 1974, Murdoch and Oaten 1975) we will limit our

discussion to one which provides a general analytical technique by which their effects on stability can be judged and which provides a summary of some of the results reported by other investigators. The analytical technique, graphical in nature, can be used for two species predator-prey models which possess an equilibrium. To illustrate, we compare the Lotka-Volterra model (eq. 2a and b) with a modification to the basic prey equation proposed by Volterra. Our discussion is based on presentations by Rosensweig and MacArthur (1963) and Smith (1974).

The stability properties of the Lotka-Volterra model are analyzed by first finding the equations of the lines for which $dN_1/dt = 0$ and $dN_2/dt = 0$.

Thus, for

$$dN_1/dt = rN_1 - \gamma_1 N_1 N_2 \quad (2a)$$

and

$$dN_2/dt = -dN_2 + \gamma_2 N_1 N_2 \quad (2b)$$

$$\frac{dN_1}{dt} = 0 \text{ when } rN_1 - \gamma_1 N_1 N_2 = 0 \quad (3a)$$

and

$$\frac{dN_2}{dt} = 0 \text{ when } -dN_2 + \gamma_2 N_1 N_2 = 0 \quad (3b)$$

By rearrangement we obtain

$$rN_1 = \gamma_1 N_1 N_2$$

and

$$dN_2 = \gamma_2 N_1 N_2$$

which after further rearrangement, simplification and cancellation gives us the desired equations

$$N_2 = r/\gamma_1 \quad (4a)$$

and

$$N_1 = d/\gamma_2 \quad (4b)$$

We can now plot these lines (Fig. 4). We note that for values of $N_1 > d/\gamma_2$, dN_2/dt is positive and for values of $N_1 < d/\gamma_2$, dN_2 is negative. Similarly, for values of $N_2 > r/\gamma_1$, dN_1/dt is positive and for values of $N_2 < r/\gamma_1$, dN_1/dt is negative. We can now insert arrows (vectors) on the graph and their resultant vector indicates the direction of the rate of changes for the composite predator-prey interactions. We can also place arrows on the $dN_1/dt = 0$ line parallel to the predator (N_2) axis and on the $dN_2/dt = 0$ line parallel to the prey (N_1) axis. These arrows (vectors) can now be joined to form a trajectory as in Figure 4 a and b. In most cases only the arrows associated with $dN_1/dt = 0$ and $dN_2/dt = 0$ are needed to indicate the nature of the stability. In the case of the Lotka-Volterra equations the analysis results in a circle which indicates that the model is neutrally stable, a well known outcome for these equations. Had the trajectory spiraled outward the model would have been unstable; had the trajectory spiraled inward it would have been stable.

In Volterra's (1926) modification of the basic Lotka-Volterra model, he simply replaced the original assumption of unlimited growth of the prey population when freed from predation to one of logistic population growth. The consequence is increased stability.

In analyzing this model we concern ourselves only with the equation for the prey population since that for the predator population remains unchanged. Again, we find the equation to the line for which $dN_1/dt = 0$. Thus, the equation for the prey population is

$$\frac{dN_1}{dt} = rN_1 \left(\frac{K-N_1}{K} \right) - \gamma_1 N_1 N_2 \quad (5)$$

$$\text{and } \frac{dN_1}{dt} = 0 \text{ where } \frac{rN_1 K}{K} - \frac{rN_1^2}{K} - \gamma_1 N_1 N_2 = 0 \quad (6)$$

Rearranging eq. 6 we get

$$\gamma_1 N_1 N_2 = \frac{rN_1 K}{K} - \frac{rN_1^2}{K}$$

which by further reductions and rearrangements yields

$$N_2 = \frac{r}{\gamma_1} - \frac{rN_1}{K\gamma_1}$$

Substituting for N_1 (eq. 4b) we obtain

$$N_2 = \frac{r}{\gamma_1} - \frac{rd}{K\gamma_1\gamma_2} \quad (7)$$

We know that equation (7) has a negative slope and that N_2 is positive when $r/\gamma_1 > rd/K\gamma_1\gamma_2$ and (by rearrangement) $K > d/\gamma_2$. We can now plot the lines for $dN_1/dt = 0$ and $dN_2/dt = 0$ keeping in mind that the arrows are parallel to the predator axis for the line, $dN/dt = 0$ and parallel to the prey axis for the line, $dN_2/dt = 0$ (Fig. 3b and c). By joining these arrows we obtain a trajectory which spirals inward towards the stationary point (the intersection of the two lines) indicating the Volterra modification stabilizes the model (Fig. 4)

We can generalize these results in the following manner using the condition of neutral stability (Fig. 4) as a frame of reference. Any factor included in the Lotka-Volterra model which rotates either or both lines (prey or predation isoclines) in a clockwise direction indicates increasing stability; rotation of either or both lines in the opposite direction indicates decreasing stability. Thus, we have a straight-forward graphical procedure for analyzing stability. Some of the modifications which have been found to improve the model's stability are: (1) prey populations are self limited (i.e., Volterra's modification discussed previously) (Smith 1974, Murdoch and Oaten 1975), (2) a constant number of prey escape the predator (refuge) (Smith 1974, Murdoch and Oaten 1975), (3) risk of the prey to predation is heterogeneous (a prey's risk of being attacked increases if it is in a high density patch) (Murdoch and Oaten 1975), (4) spatial heterogeneity when different subpopulations have different parameter values of predator and prey (Murdoch and Oaten 1975), and (5) a sigmoid-shaped functional response curve over a portion of its range (Murdoch and Oaten 1975). Detailed treatment is found in May (1973), Smith (1974) and Murdoch and Oaten (1975).

4. Rosenzweig-MacArthur predator-prey model.

Rosenzweig and MacArthur (1963) and Rosenzweig (1969) propose a more general predation model using the graphical technique described above. They argued that the prey isocline (the line on the graph which delineates the set of points at which the rate of growth, dN_1/dt is zero) is humped as in Figure 5. This implies that the prey's growth rate at low densities is facilitated by increasing prey density. Such social facilitation might imply that a minimum number of individuals are necessary to

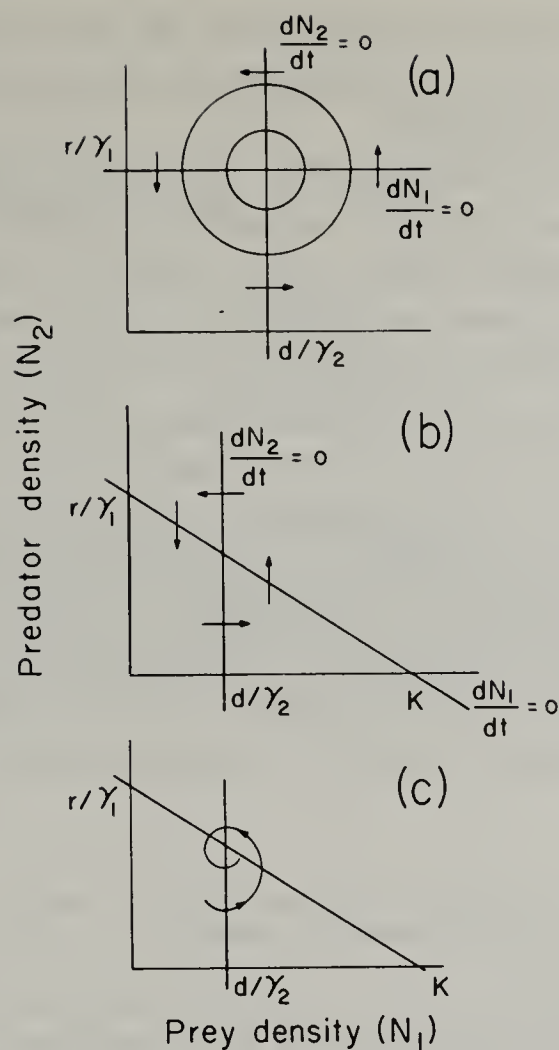


Fig. 4.—Graphic illustrations of Lotka-Volterra models explaining (a) neutral stability, (b) and (c) stability (see text).

most efficiently exploit a resource. In contrast, the predator isocline is similar to the one we have previously seen, with the difference that at some upper predator density a factor such as limited space, territoriality other mutual interference causes the predator population to be limited at a maximum density even with abundant unexploited prey.

They point out that if the predator isocline is to the right of the hump the interaction between predator and prey is stable; if it is to the left the interaction is unstable. A humped prey isocline is suggested by Huffaker's (1958) *Typhlodromus occidentalis* (predator)/*Eotetranychus sexmaculatus* (prey) interaction as analyzed by Rosenzweig (1969). Further, Maly (1969) in laboratory experiments, found a humped prey isocline, with the predator isocline to the left of the hump, for an *Asplancha* (rotifer predator)/*Paramecium* interaction. This type of predator-prey interaction (predator isocline to the left of the hump in the prey isocline) implies that an efficient predator

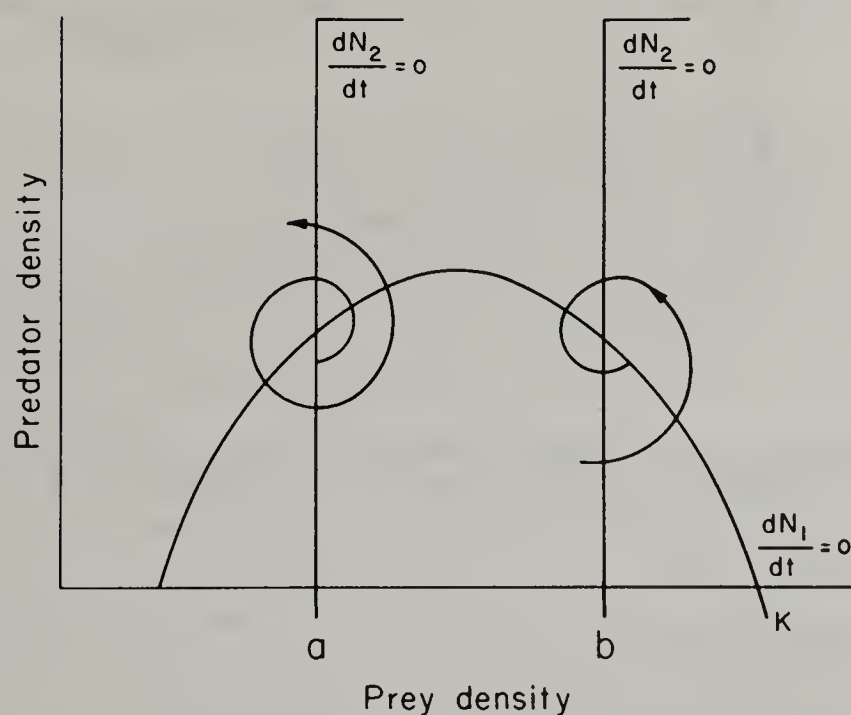


Fig. 5.—Graphical representation of the “humped” prey isocline with the predator isocline to the left of the “hump” ($dN_2/dt = 0$ intercepting the x-axis at a) resulting in an unstable predator-prey interaction, and the predator isocline to the right of the “hump” ($dN_2/dt = 0$ intercepting the x-axis at b) resulting in a stable interaction. K is the environmental carrying capacity.

species (one which could survive and reproduce at low prey densities), could drive the prey population to local extinction. Such extinction would be prevented, however, if a proportion of the prey remained unavailable to the predator.

Ricklefs (1973) presents a summarization of those features which contribute to a non-linear prey isocline and the type of non-linearity evidenced. Ricklefs (1973) also presents a summarization of a number of realistic features (e.g., immigration, refuges, mating inefficiency at low prey densities) which contribute to a non-linear prey isocline and determine whether the slope is negative or positive (Fig. 6). He also presents a similar summarization for the predator isocline (Fig. 7). This compares to the linear horizontal prey isocline and the linear vertical predator isocline (dashed lines Figs. 6 and 7) which are assumed in the basic Lotka-Volterra equation. The increasing complexity of factors incorporated by Ricklefs (1973) in his graphical summaries are among those that biological control specialists have long recognized as essential in appraising, empirically, the role of natural enemies in their native areas or their prospects for effectiveness after their introduction into new areas. These models, then, in one sense may be viewed as representing what biological control specialists have intuitively felt; that the stability of a predator-prey or host parasite interaction is related to a wide variety of factors, many of them not utilized in explicit predator-prey models, and extrinsic to the specific interaction.

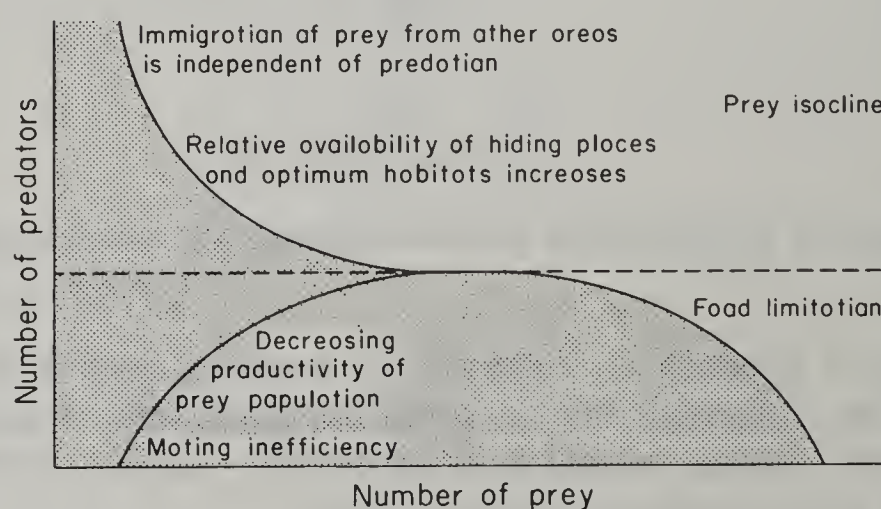


Fig. 6.—Graphical representation of the prey equilibrium isocline, incorporating several biological properties of natural systems. The isocline for the Lotka-Volterra equation is indicated by a dashed line. (After Ricklefs 1973)

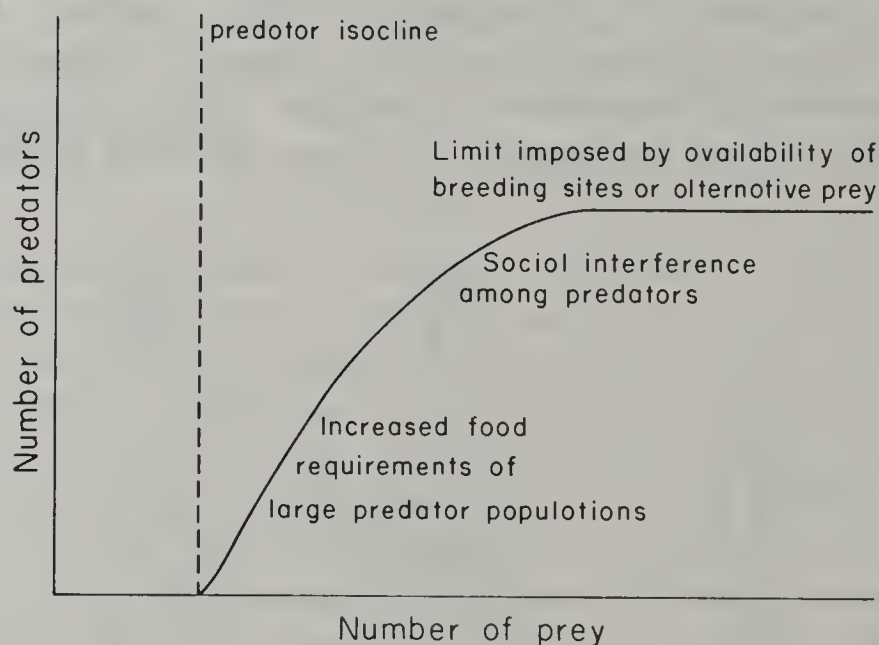


Fig. 7.—Graphical representation of the predator equilibrium isocline, incorporating several biological properties of natural systems. The isocline for the Lotka-Volterra equation is indicated by the dashed line. (After Ricklefs 1973)

5. Functional response models

An individual predator's response to increasing prey density can be classified into one of 3 types (Holling 1959b, 1965, 1966) (Fig. 8). Collectively, they are referred to as the functional (or behavioral) response of a predator, which is defined as the rate of change in an average predator's attack-rate with variations in prey density (Hassell et al. 1976). Solomon (1949) formalized the

distinction between this type of predator response and the response in predator numbers (numerical response).

Laboratory experiments have indicated that the “typical” functional response for parasitoids and predators is type 2 (Fig. 8) (Murdoch and Oaten 1975, Hassell et al. 1976) which can be described by the ‘disc equation’ of Holling (1959b):

$$N_1 = \frac{a' T N_o P}{1 + a' T_h N_o} \quad (8)$$

where N_o is the initial number of prey (hosts); N_A , the number of prey (hosts) attacked; T_s the total time the predator (parasite) spends searching for prey (hosts); T_h , the time required to handle the prey (hosts), including the time spent pursuing, subduing, eating and digesting each prey; P , the number of searching predators (parasites); and, a' , the attack rate of the predators (parasite).

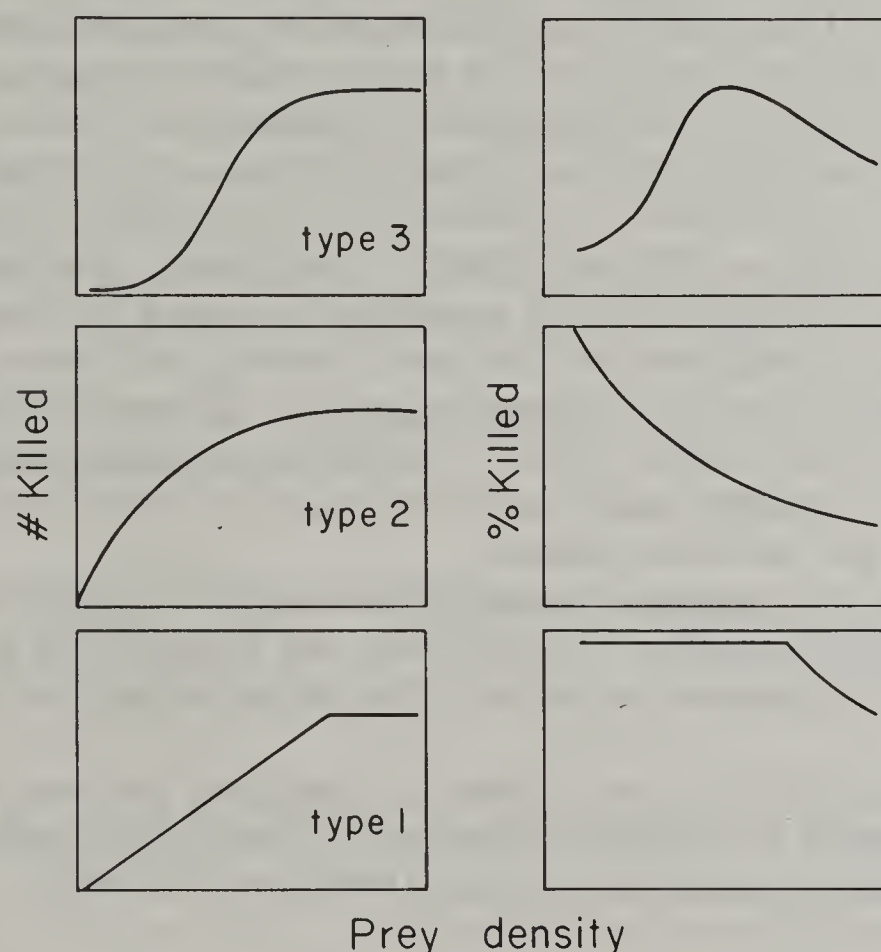


Fig. 8.—Three types of functional response designated by Holling (1959). For each type the number (and percentage) of prey killed per unit time by a single predator is graphed against prey density. Only type 3 yields density-dependent mortality.

Royama (1971) and Rodgers (1972) discuss the assumptions upon which this model is based, and consider it crucial from an experimental point of view that the model makes no allowances for decreasing prey density as prey are consumed. Therefore, laboratory experiments must be carefully designed to replace the eaten individuals or to ensure that the number of hosts (prey) eaten are less than 10% of the total available (Murdoch and Oaten 1975). Should the experiment not meet these criteria then eq. 8 must be incorporated into one of the exploitation models provided by Rodgers (1972) (see also Hassell et al. 1976).

The “disc equation” (8) has been used to evaluate the attack behavior of parasites (e.g., Messenger’s (1968) studies on the influence of temperature on attack rate a' and functional response of *Praon exosoleum* (Nees), an introduced parasite of the aphid *Therioaphis maculata*). Use of handling time, T_h , to characterize parasite-host interactions, however, presents some problems. Holling (1965, 1966) applied handling time to predators and considered it to include the time required to pursue, subdue, consume and digest a prey; thus, the concept implies hunger. Messenger (1968) and others have considered the time between egg deposition in a host and the resumption of searching by a parasite to be homologous with the digestive pause of a predator. Clearly, this is inappropriate. The process of digestion and the return of hunger in a predator are both intrinsically

related to the previous attack(s), whereas the parasite's lack of available eggs for oviposition is dependent upon the inherent egg supply, the stage of development of the eggs, the age of the female parasite and the number of eggs she has already laid, all of which are not so related. For example, the California strain of *Venturia* (= *Nemeritis*) *canescens* (Grav.) can only lay ca. 26 eggs/day (Matsumoto and Huffaker 1973, Stinner 1970); thus, on the average, only 1.1 eggs/hour are available for oviposition. Since 20 seconds are required for oviposition (Hassell and Rodgers 1972), the parasite's limited egg supply would be exceeded if it encountered more than 1.1 suitable hosts per hour. The time required for oviposition, then, represents only a very small proportion of the parasite's handling time if the latter includes the delay caused by the lack of available eggs.

Analysis of models containing one of the three types of functional response shows that a type 3 response provides stability, while types 1 and 2 are destabilizing (Holling 1965, Hassell and May 1973, Murdoch and Oaten 1975). It is, however, the type 2 response which characterizes the majority of predators and parasites tested in the laboratory (Murdoch and Oaten 1975, Hassell et al. 1976). It is worth noting that many of these experiments failed to consider lack of specificity, thereby implying that the entomophage was monophagous. Although some certainly are, on theoretical grounds it can be argued that parasites or predators which are not host specific may stabilize prey populations by "switching." Murdoch and Oaten (1976, p. 104) state that predators (parasites) that show weak *average* prey preferences at equal prey ratios, but whose preferences vary greatly among individuals, subsequently switch to other prey when presented with unequal prey ratios. When they incorporated switching into Holling's disc equation they sometimes obtained a type 3 response although the model was "rather awkward and encumbered by assumptions." They also constructed a model based directly on a switching mechanism. Although "rather complicated," the model predicted that a type 3 functional response is most likely to occur if a predator's tendency to eat a prey is greatly increased when its last meal was an individual of the same species, and when the prey species under consideration is not abundant but the alternative prey is. Thus, switching by an oligophagus or polyphagus natural enemy may change a type 2 functional response to a type 3. The implication, then, is that a tendency for stability might thus be enhanced, but other features of the predator-prey (parasite-host) interaction will also be important.

Ultimately, however, the predator's (parasite's) *numerical* response will determine whether a predator-prey (parasite-host) interaction is stable. Thus, the presence of a type 2 functional response can by no means be used to dismiss a potential biological control agent as incapable of regulating its host.

It is the numerical response, more so than the functional response, per se, by which natural enemies are able to overtake in numbers, suppress and eventually regulate their prey's (host's) populations (a coupled, delayed numerical response) (Huffaker et al. 1971).

6. The Nicholson-Bailey Model

Up to this point we have been discussing models which theoretically relate to organisms exhibiting continuous rates of population growth. We now deal with those which relate to organisms which display periods of reproduction. Interestingly, they have more appeal to the field entomologist because they reflect better his experience with insect populations, which do not reproduce continuously. Nicholson and Bailey's (1935) equations represent such a model and were specifically formulated to characterize an insect parasite-host interaction. Their equations can be written:

$$H_{(t+1)} = H_{(t)} F e^{-aP_{(t)}} \quad (9a)$$

$$P_{(t+1)} = H_{(t)} (1 - e^{-aP_{(t)}}) \quad (9b)$$

where $H_{(t)}$, $H_{(t+1)}$, $P_{(t+1)}$, and $P_{(t)}$ are the densities of the host and parasite in successive generations; F , the net reproductive rate of the host (fecundity less all other losses save that caused by the parasite) and, a the "area of discovery" of the parasite.

Many of the assumptions upon which the Nicholson-Bailey model is based are the same as those for the Lotka-Volterra equations: the parasite *population* is assumed to search at random changes in

parasite or host density do not affect the parasite's attack-rate, the host's fecundity and also its mortality by other factors than parasitism are assumed to be constant and, finally, the parasite is assumed to have an unlimited egg supply. It differs from the basic Lotka-Volterra equation in that it includes time lags for host and parasite development (incorporated in the model through use of difference equations).

Although not widely appreciated, the Lotka-Volterra and the Nicholson-Bailey models are homologues of one another. If the Lotka-Volterra equations are rewritten in a difference equation format, they are basically the same as those for the Nicholson Bailey model. The former equations can be written (changing the notations of May (1972) as follows:

$$H_{(t+1)} = H_{(t)} F(1-aP_{(t)}) \quad (10a)$$

$$P_{(t+1)} = H_{(t)} F(aP_{(t)}) \quad (10b)$$

The only difference between the two models (equations 9a-b and 10a-b) is the way in which the parasite (predator) attack coefficient is incorporated, but this difference has no effect on the model's stability. Analysis of these models shows them both to be unstable and their instability is due to the time-lags implicit in the difference equations. The implication, then, is that time lags are destabilizing and it is this feature which is the major distinction between the classic Lotka-Volterra (eq. 2a and b) and Nicholson-Bailey (eq. 9a and b) models.

It is also worth noting that stability of a model formulated with difference equations implies stability of its differential homologue, although the converse does not hold (Murdoch and Oaten 1975).

The steady densities (equilibrium densities) of the parasite and host can be calculated from the canonical form of the equations (see May 1972):

$$H_{(t+1)} - H_{(t)} = H_{(t)} (F \exp [-a P_{(t)}]) - 1)$$

and

$$P_{(t+1)} - P_{(t)} = H_{(t)} F (1-\exp[-a P_{(t)}]) - P_{(t)}$$

where by definition $(H_{t+1} - H_t)$ and $(P_{t+1} - P_t)$ equal zero. The steady state equations are

$$H^* = \frac{1nF}{a(F-1)} \quad (11a)$$

and

$$P^* = \frac{1}{a} 1nF \quad (11b)$$

where H^* and P^* connote respectively the steady densities of the host and parasite populations. An analysis of this equilibrium point shows it to be unstable, leading to growing oscillations and eventual annihilation. The instability of the model was recognized by Nicholson and led him to propose that, in nature, interacting subpopulations of parasites and hosts may become locally extinct but because the many subpopulations act asynchronously with respect to the particular theory," though readily phase of a cycle each is in, the population as a whole would persist. This fragmentation though phase of a cycle each is in, the population as a whole would persist. This fragmentation though readily observed in nature, is of course unsatisfactory as an explanation of population regulation. Nicholson made no attempt to model it and has said (personal communication) he did not see how it could be done. The specific model failed to mimic the host regulation frequently observed when a natural enemy has become successfully established. Thus, the Nicholson-Bailey model left us with no better inherent

insights into the basic predator-prey/host-parasite interaction than are found in the Lotka-Volterra model.

7. The Hassell and Varley modification of the Nicholson-Bailey model.

Hassell and Huffaker (1969), while analyzing a *Venturia canescens*/Mediterranean flour moth (*Ephesia kuhniella* Zell.) interaction noted that the "area of discovery" of *V. canescens* varied with changes in parasite density. Ulyett (1950) and Huffaker and Kennett (1969) referred to this effect as a mutual interference phenomenon. Hassell and Varley (1969) found this to be a common feature of the host-parasite interactions they reviewed, and proposed a regression model to describe the relationship. Their regression model relating area of discovery to parasite density can be written:

$$\log a = \log Q - m \log P_{(t)}$$

or

$$a = QP^{-m}. \quad (12)$$

Substituting equation (12) for a in the basic Nicholson-Bailey equations (eq. 9a and b) gives the following:

$$H_{(t+1)} = H_{(t)} e^{-Q P_{(t)}^{1-m}} \quad (13a)$$

$$P_{(t+1)} = P_{(t)} (1 - e^{-Q P_{(t)}^{1-m}}) \quad (13b)$$

where Q is the "quest constant" or the "area of discovery" when the parasite density is unity and m the mutual interference constant (an intraspecific competition factor) of the parasite. All other symbols are the same as for equations (9a and b). The equilibrium densities for the populations are:

$$H^* = \left[\frac{F \ln F}{Q(F-1)} \right]^{\frac{1}{1-m}} \quad (14a)$$

$$P^* = \left(\frac{1}{Q} \ln F \right)^{\frac{1}{1-m}} \quad (14b)$$

Analysis shows the model to be stable for certain values of F and m (Fig. 9) (Hassell and May 1973). Interestingly, the model predicts that increasing its stability by increasing the value of m (for values of $m < 1.0$) at a given value of F leads to higher steady densities for both host and parasite populations. The model also suggests two other consequences of significance to biological control. First, the model mimics certain observed features of a successful biological control project. The introduction of a small number of parasites against a dense pest population leads to a stable interaction provided an intraspecific competition (here m) of sufficient magnitude exists. As the value of m approaches zero the Hassell-Varley model simplifies to the basic Nicholson-Bailey equations. Secondly, the model provides for coexistence of two parasite species on the same host population, a feature usually observed in nature. However, the coexistence of two parasite species only occurs at a limited set of values of Q and m for both species; otherwise, one of the two species, one will displace the other.

It should be noted that Q , like a of the Nicholson-Bailey equations, is not really a constant. This was recognized by Varley et al. (1974) following work of Royama (1971), Rodgers (1972) and Hassell and May (1973). The value of Q can be affected by handling time and/or a limited egg supply of the parasite, especially at higher host densities.

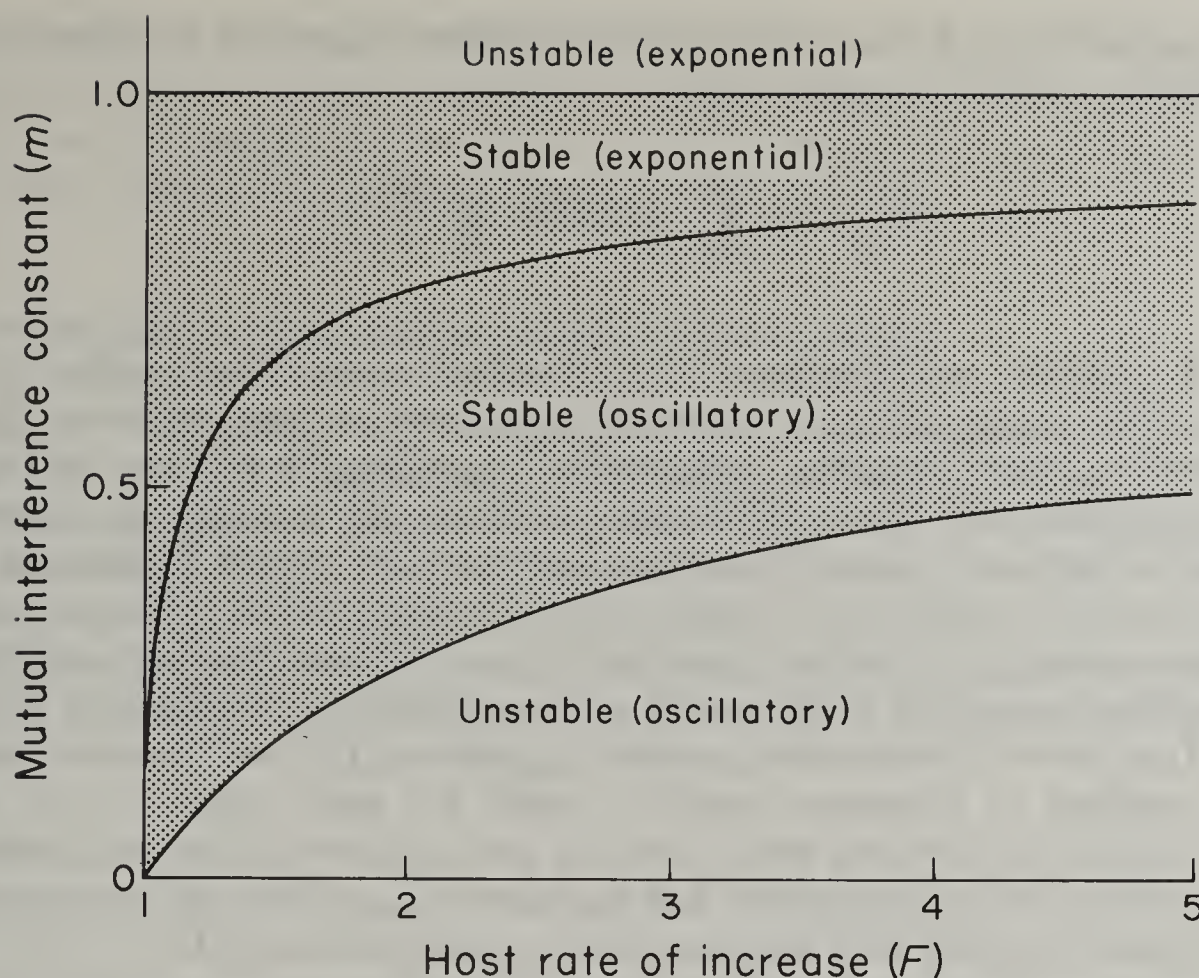


Fig. 9.—Stability boundaries between the mutual interference constant (m) and the host rate of increase (F). The shaded area denotes the conditions for stability and is divided into two regions (1) where the equilibrium host and parasite populations are approached exponentially; and (2) where there are damped oscillations. The line between these regions indicates the conditions for most rapid approach to the equilibria. (After Hassell and May 1973)

8. Some additional host-parasite models.

Hassell and May (1973) explored three models built upon those of Nicholson and Bailey (1935) and Hassell and Varley (1969). The first explored the consequences of adding the functional response of Holling's disc equation to the Hassell-Varley model (eq. 13a and b). This was accomplished by making the total time (T_t) dependent on parasite density such that:

$$\frac{H_a}{P_t} = \frac{a' T_t c P^{-m} H_t}{1 + a' T_h H_t} \quad (15)$$

where H_a is the number of attacked hosts; c , a constant and the remaining symbols are as before; ($a T_t c$ can be thought of as a modified Quest constant, Q). The assumptions upon which this model is based are the same as those for the Hassell-Varley and "disc equation" models. It should be noted that the model simplifies to Holling's disc equation in the absence of mutual interference ($m = 0$) and to the Hassell-Varley equation if the handling time is nil ($T_h = 0$).

Their analysis of the model indicates that three parameters significantly affect its stability: (1) a complex parameter which represents "handling time," (2) mutual interference (m) and (3) the net rate of increase of the host (F). Increasing the "handling time" for any given set of values for mutual interference and net host increase reduces the model's stability. Similarly, for any given set of "handling time" and mutual interference values, increasing F (the net rate of host increase) also destabilizes the model. However, Hassell and May argue that handling time is only a very small fraction of the parasite's total searching time; hence, it is not likely to significantly affect the stability of the host-parasite interaction. Mutual interference appears much more important and it is a powerful stabilizing influence.

Secondly, these investigators (Hassell and May 1973) explored the consequences of spatial heterogeneity on stability of the parasite-host interaction by dividing an area into n subunits and distributing hosts and parasites among them according to the criteria, a_i the proportion of hosts in

the high density subunits and β_i the proportion of parasites aggregated in subunits with high host densities. The particular model they chose was:

$$H_s = H_t \sum_{i=1}^n [a_i \exp(-a_i \beta_i P_t)] \quad (16)$$

which distributes P_t parasites and H_t hosts into N_i subunits in proportions specified by a_i and β_i . The model is based on several assumptions which are: (1) that there are only n subunits through time and for every generation a_i and β_i describe, respectively, the allocation of hosts and parasites in the subunits. This implies that the same distribution of hosts and parasites are reconstituted every generation, (2) that within each subunit the parasite assumes the role of a Nicholson-Bailey parasite and (3) that parasites do not search empty subunits (i.e., units in which there are no hosts) and that an individual parasite spends all of its time searching only one subunit (Murdoch and Oaten 1975).

When the stability properties of the model were analyzed, four trends were identified (Hassell and May 1973). They were (1) increasing parasite aggregation (β_i) will increase stability and this factor alone can stabilize an otherwise unstable model, (2) with respect to the particular host distribution used, stability is increased when there are more regions of low host density, (3) a wider range of stability exists when approximately half the hosts occur in high density areas (subunits) and (4) stability breaks down abruptly with increasing net reproductive rate (F).

Finally, a model was developed which combines spatial heterogeneity of the host, aggregative behavior of the parasite and density effects of the parasite (mutual interference, m) and was used to explore their combined effects on the stability of a host-parasite interaction. They accomplished this by combining the previous model (eq. 16) with the host equation (eq. 13a) of the Hassell-Varley model, which leads to the following result:

$$H_s = H_t \sum_{i=1}^n (a_i \exp(Q \beta_i P_t^{1-m})) \quad (17)$$

where the symbols are defined as before. The only assumptions which differ from the previous model is that, (1) the parasite assumes the properties of a Hassell-Varley model parasite, i.e., one which is subjected to mutual interference and (3) mutual interference can be represented by a single constant.

An analysis of this model led Hassell and May (1973) to conclude that only modest levels of parasite aggregation (β_i) and mutual interference m were necessary to impart a high degree of stability.

Murdoch and Oaten (1975) also explored spatial heterogeneity by investigating the stability properties of a differential equation model which required a predator to spend time traveling between patches (transit time), searching empty patches and handling prey. They concluded that transit time adds stability to a predator prey interaction, the greater the transit times the more stable the interaction. This might account for the greater degree of stability exhibited by Huffaker's (1958, 1963) predator-prey interactions when physically complex systems, in contrast to simple ones, were used. A number of other investigators have noted that temporal or spatial asynchrony can contribute to more stable host-parasite, prey-predator interactions. Bailey et al. (1962) found results similar to those of Hassell and May (1973) discussed above. Griffiths (1969), Hassell (1969) and Hassell and May (1973) have suggested that modest amounts of asynchrony between host and parasite can impart stability to such an interaction. Finally, Auslander et al. (1974), using a differential

A final thought is worth contemplating. Murdoch and Oaten (1975) concluded from their analysis of various models that the results were consistent with the claim that a major aspect of diversity which promotes stability in both model and simplified systems (such as laboratory and agricultural systems) is spatial heterogeneity rather than species diversity. Since natural systems with few species can be stable, we wonder whether our claim about spatial heterogeneity in simplified systems may not also apply to natural systems. To this conclusion we would add that perhaps species diversity, because of the specific coevolved linkages and temporal heterogeneity conferred, may also present important aspects of stability through diversity. Finally, it is also clear that intraspecific competition among hosts (the logistic equation added to the Lotka-Volterra model discussed previously, or the addition of a direct density-dependent factor acting on the host in a

Nicholson-Bailey model (Huffaker and Stinner 1971)) or in parasite populations (mutual interference (Hassell and Varley 1969)) or density-dependent movements among subunits of habitat (Huffaker and Stinner 1971) are also stabilizing. Thus we see that the general behavior of these models confirms the biological control specialist's intuition, that it is the complexity of the interactions which is important.

9. A general population model incorporating biological control.

Varley et al. (1974) developed a model which incorporated a number of other mortality factors besides that due to a parasite. It is basically an extension of the Nicholson-Bailey, Hassell-Varley equations. They used this general approach to develop a model of the biological control of winter moth, *Operophtera brumata* (L.), in eastern Canada, which resulted from the introduction of two parasites, *Cyzenis albicans* (Fall.) and *Agroypon flaveolatum* (Grav.). The model was developed from the 13 years of data collected by these workers in England, with additional laboratory investigations and analysis of the Canadian data (Embree 1965). Their models for the winter moth, *Cyzenis* and *Agrypon* were:

a. for the winter moth:

$$\log N_{n+1} = \log N_n - k_2 - k_3 - k_4 - k_1 + \log F \quad (18)$$

b. *Cyzenis*

$$\log P_{n+1} = \log [N_n (1 - \exp(-QP_n^{1-m}))] - k_4 \quad (19)$$

c. *Agrypon*

$$\log P_{n+1} = \log [N_s (1 - \exp(-QP_n^{1-m}))] - k_4$$

where

- k_1 = Mortality during the egg and larval stages, excluding parasitism which was assumed to be a constant ($k_1 = 1.6$) and the mean of the observed values from Embree (1965)
- k_2 = Mortality due to *Cyzenis* [$k_2 = (0.056P^{1-0.52})/2.3$]. Since handling time was short and egg supply large the parasite submodel does not include any effects of host density on searching efficiency [$k_2 = (QP^{1-m})/2.3$].
- k_3 = Mortality due to *Agrypon*. No information is available on this parasite species so the model assumed it has the same characteristics as *Cyzenis* (above) but had a limited egg supply of 100 eggs/female [$k_3 = (QP^{1-m}/2.3)$].
- k_4 = Pupal mortality assumed to be a constant ($k = 0.2$) and much less in the Canadian than in the English populations. Since the parasites occur within the body of this host and over-winter in the soil along with the winter moth pupae it was assumed they experience the same mortality as the moth pupae.

The model's results are plotted in Fig. 10.

In comparing the model with the Canadian population data (Embree 1965, 1966, 1971), they found these results mimicked the population declines observed in Nova Scotia following the parasites' introduction. They obtained a stable interaction but this model predicted a decline in the winter moth population 1 year later than was observed in Canada. Furthermore, a gradual increase in the winter moth population was then also predicted, which has yet to be observed in the actual populations.

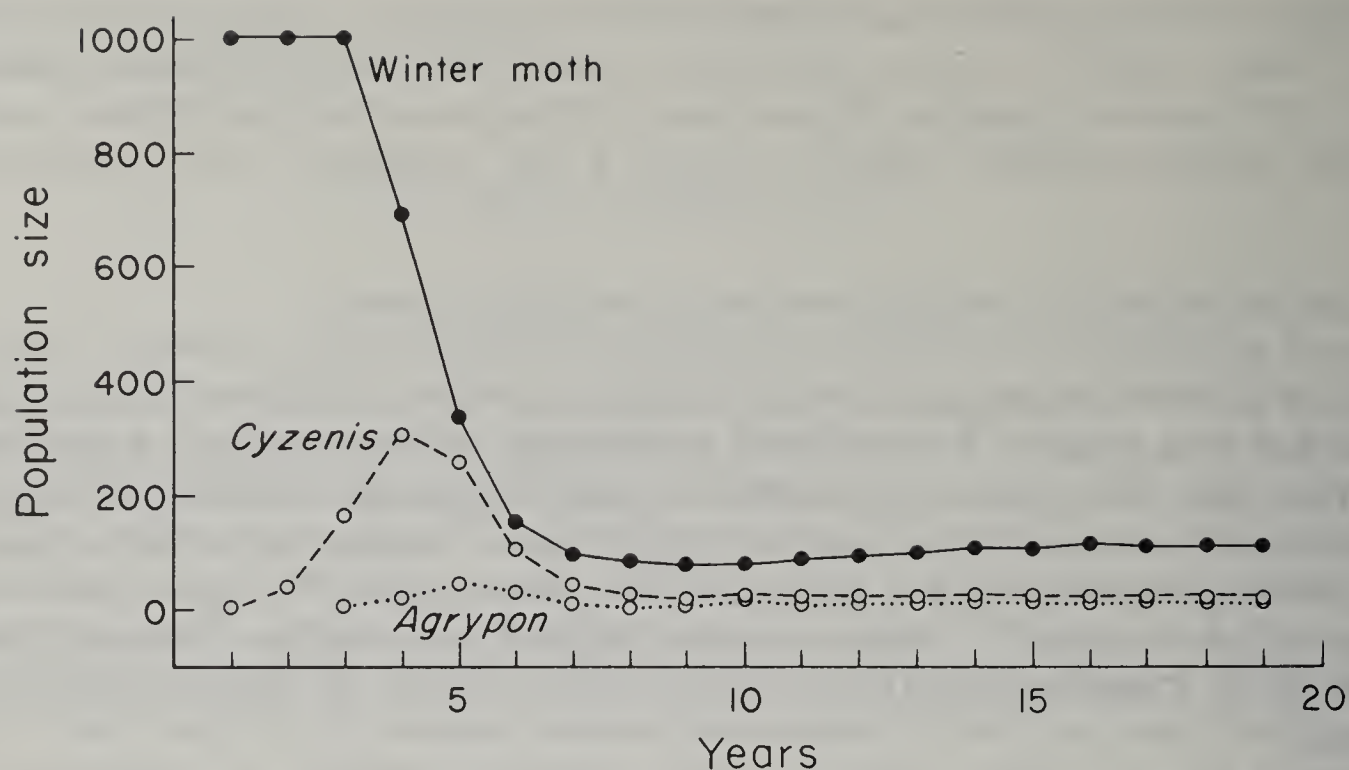


Fig. 10.—Host-parasite model simulating the biological control of winter moth by *Cyzenis* and *Agrypon* in Nova Scotia (see text). (After Varley et al. 1974)

10. *Desiderata from the above models concerning a good biological control agent.*

Hassell and May (1973) identified three basic parasite responses which have marked effects on the host-parasite interaction. They were, (1) the functional response to host density; (2) the response to parasite density (mutual interference); and (3) the response to host distribution. They then suggested that in searching for a parasite to introduce for biological control those which have the following characteristics are the more likely to stabilize their host population at low densities: (1) a high intrinsic searching efficiency which is necessary to attain low equilibrium densities. (2) A small handling time (T_h) relative to the total adult searching time. This will minimize the instability which results from the functional response. (3) A degree of mutual interference (m) in the range $0 < m < 1$ which contributes to stability. (4) A high level of parasite aggregation with respect to the host distribution — the more even the host distribution the higher the parasite aggregation needed.

Even though Hassell and May suggested these searching characteristics they realized that other factors affect the success of a biological control agent — such things as a favorable climate, synchronization and host specificity (see Section II above). Thus, without a clear set of all the criteria for deciding which parasite to introduce it seems of little value to expend scarce resources extensively investigating a parasite's searching characteristics prior to introduction. Our quantitative understanding of the parasite-host interaction has yet to reach the level at which it can replace current practices (with proper safeguards) based upon the general biological properties required of natural enemies (Section II) and the empirically derived evidence (e.g., has a parasite exhibited good control elsewhere?).

The biological control model developed by Varley et al. (above) sheds additional light on these questions. The value of this model is that it incorporates field data (from life tables), thereby assessing the consequences of variability in certain population processes related to mortality (Varley and Gradwell 1970, Varley et al. 1974). From the winter moth example, Varley et al. (1974) concluded: "Perhaps the most important aspect of this model is that it indicates how much preliminary study is required to produce a model which is likely to predict the outcome of a biological control program. The searching parameters of parasites can be obtained by careful laboratory experiments, but it is not known how these relate to searching under field conditions. An adequate sub-model for parasitism, however, is not sufficient. The winter moth example has shown how critical other components may be. In this case it is the absence of a strong density-dependent pupal mortality that largely accounted for the [formerly] high winter moth populations in Canada and then permitted *Cyzenis* populations to increase to very effective levels. Such information is best obtained by a detailed census converted to life tables, but this may prove too lengthy a process, especially when there is only one generation of the host insect per year. Only if factors affecting the

survival of both host and parasite in the field have been adequately quantified can we develop satisfactory predictive models for use in biological control.”

Since such lengthy life tables would have to be developed for each case proposed for biological control, they seem of limited practical value. Rather, their value lies in evaluating introductions so that insights into those features which affect a program's success might be gained. An evaluation of a few well chosen examples might help us to more explicitly define the attributes of a desirable natural enemy for biological control and suggest methods for their identification prior to introduction. However, it is unlikely that models will ever be able to replace experience entirely; rather, they may serve to supplement it.

However, pre-introduction investigations are essential to determine (1) the climatic similarities between the indigenous and target areas; (2) the taxonomic status of the indigenous host relative densities. If so, this implies that the natural enemy may be regulative in the indigenous area and capable of being so in the target area.

Whether pre-investigations, however thorough, can provide enough information to judge in advance the probable outcome of an introduction remains controversial. For example, Varley et al. (1974) argue that enough is known about the importance of the principal searching characteristics (a, m, β) that evaluating a natural enemy for these characteristics should give us some improvement in predicting the probable success of an introduction. In contrast, Way (1973) argues that “It is probably unlikely that we will ever be able to predict with accuracy the consequences of introducing a particular natural enemy or of manipulating a particular part of the environment to favor indigenous natural enemies.” Further, Simmons (1972) noted that a carefully selected species may, on introduction into a new area with a somewhat different climate, flora, and ecology, react in an unpredictable way and be a failure while an unpromising one may be a success. Finally, DeBach (1974) points out that although we can gain some insights from careful studies in the field and laboratory, “How to put everything together to choose a potentially effective enemy beforehand with certainty is still beyond our grasp.” Of course Varley et al. (1974) did not imply it could be done with certainty.

Thus it remains unclear as to how extensive pre-introduction investigations should be or how valuable they might be in identifying candidate species with a high probability of success, although many specialists argue for some pre-introduction evaluation. Of course investigations are necessarily much more extensive for phytophagous species proposed for biological control agents of weeds, but for reasons of safety.

It is important to note that stability, however defined, is not the only important feature which determines the success of a host-parasite interaction. Many factors other than those responsible for stability cause variations and fluctuations in population densities. These fluctuations are of as much concern to the applied ecologist as is the stability. Finally, if the population densities of the pest resulting from a stable, host-parasite interaction, rise above those tolerated by the economics of the crop, then stability is of little practical value. Thus stability is only one of many criteria by which the dynamics of a host-parasite interaction should be judged.

Habitat Manipulation to Achieve Improved Biological Control

Manipulating a habitat to achieve more effective biological control from introduced or resident natural enemies implies an understanding of the basic ecology and dynamics of both the pest and natural enemy populations. It has long been a cherished idea of ecologists that community diversity lends greater stability to the system and frequently, by such diversity, is meant only the number of species present. As has been pointed out by many authors, this is not necessarily so, especially in agriculture (Southwood and Way 1970, Huffaker 1974, van Emden and Williams 1974, Murdoch 1975 among others). As Southwood and Way (1970) note it very much depends on whether one is referring simply to number of species per se or whether the increase means an increased number of species at higher trophic levels (trophic diversity). On the basis of rather simplistic theoretical models (Lotka-Volterra multispecies models – see Section III) May (1973) concluded that greater trophic diversity provides no more stability than a single predator-prey interaction, although Southwood and Way (1970) stated that the question of whether trophic diversity promotes stability depends upon the habitat's climatic stability and the precision of the response of any particular trophic link to increases in the populations of those organisms composing the lower level. Furthermore, Murdoch (1975) and van Emden and Williams (1974) summarize evidence which indicates that there is no

convincing field evidence that natural communities with more species are more stable than those with less.

The artificial nature of an agricultural system is usually pointed to as evidence of instability because it has fewer species. But this appears an improper comparison (Murdoch 1975). Perhaps the most important difference between natural and artificial (agricultural) communities is that the species composing the artificial ones have not co-evolved together. Thus, simply adding just any species of enemies that can survive will not help to stabilize an agricultural community; it is those with co-evolved linkages (i.e. rather host specific natural enemies) that are desired to produce stability.

There are examples of adding or subtracting elements from an agro-community that show both detrimental and beneficial effects on pest management. Hedgerows with flowering plants can both increase certain parasite species and increase the fecundity of the cabbage fruit fly (Southwood and Way 1970). Furthermore, manipulating plants present in and around a crop has been shown to be a way of controlling pests. For example, Douthett and Nakata (1965) showed the effectiveness of planting blackberries near grapes to provide a parasite of grape leafhopper with an essential alternate host. Stern et al. (1976) suggested interplanting rows of alfalfa in cotton as a means of controlling *Lygus hesperus* Knight. These sorts of ad-hoc habitat manipulations are unlikely to be suggested by modeling. As Way (1973) points out there appears to be far too much emphasis being placed on life tables and modeling at the expense of some rather pragmatic, ad-hoc experimental habitat manipulation and other studies. One aim of pest management should be to determine what elements of an environment need to be retained and what need to be eliminated to enhance the management of a pest's population (Southwood and Way 1970).

Enough has been said in Section II to suggest the need for securement of better information concerning possibilities of using alternative hosts or footstuff, nesting sites, or of making strategic seasonal releases, or, even, release of the pest itself as a means of obtaining continuity of a natural enemy during a critical period (e.g. Huffaker and Kennett 1956, Parker 1971, Hussey and Bravenboer 1971).

Guidelines and Conclusions

The following general guidelines to improve the prospects for a successful biological control project are suggested:

1. Increase effort in foreign exploration and concentrate this effort in areas climatically comparable to the target area(s).
2. Seek strains (i.e., a genetic spectrum) of natural enemies well adapted to the species or strain of the host for the whole host range in the target area.
3. Conduct studies when feasible over a few host generations in the field to ascertain the best species on which to put major effort in terms of establishing the species most capable of regulating the host (or prey) at low host densities. Check-methods for evaluation of impact and studies of numerical response potentials at different host densities could be conducted under field conditions in the source area.
4. At present, and for the foreseeable future, the only practical approach to obtaining the best natural enemy for a given habitat or the best combination of species for that habitat or for the entire host range is to introduce a complex of primary natural enemies.
5. If an order of priority in effort is necessary, first emphasis should be given to parasites possessing high searching capacity; this will mean commonly, those which possess appropriate density responsive searching characteristics and are most effective at low host density, and ones which are intrinsically inferior but extrinsically superior competitors.
6. In general, parasites or predators possessing high host specificity or capacity to develop high preference for the target species, should be favored, especially for a permanent regulatory role in long-lived stable habitats — i.e. they should possess high K-strategy make-up.
7. Greater attention should be given to introduction of species possessing higher r-strategy make-up — e.g., predators having greater range of acceptable prey and higher mobility from habitat to habitat, for use in short-lived frequently disturbed habitats such as annual row crops. Caution should be used in considering their introduction, however.
8. Greater attention should be given to introductions of natural enemies lacking excellent capacities for permanent host regulation, in event the latter is not possible, e.g. where ones effective

otherwise cannot survive the winters in the target area but which offer possibilities for yearly spring releases for control that season.

9. Apart from introductions, basic biological and ecological studies on the various intricacies of the host-parasite or predator-prey relationship should be undertaken in the field. These studies should consider the capabilities of effectiveness of resident natural enemies in the target habitat, the means of manipulating the habitat, the host species, and the indigenous or introduced natural enemies in order to improve their biological control effectiveness. New developments offer considerable possibilities in these respects quite independent of the insights gained from the type of modeling dealt with above.

10. No type of pest problem, or habitat, or geographic area, should be considered beyond the possibilities of biological control, although this tactic is not likely to be adequate for every problem or crop situation, and will commonly be employed in combination with other tactics in an integrated control approach.

Biological control specialists should follow closely the efforts to analytically determine those searching characteristics of a natural enemy which inherently result in lower host density (mainly searching efficiency) and those which contribute to stabilize the interaction at low host density, e.g., combinations of searching capacity, handling time, mutual interference, and aggregative tendency appropriate to the host density distribution pattern. They should also more fundamentally explore the roles of extrinsic stabilizing processes heterogeneity and movements within and between subhabitat units. It may thus prove feasible to revise the guidelines given above, items 1 to 10.

Lastly, the situation of biological control is much more complex than the action of drugs on the single human species. Yet, Ludwig and Potterfield (1971) concluded that it is "... difficult to predict biological activity on the basis of chemical structure ... consequently the testing and evaluation of drugs *remains* pragmatic". Moreover, the successful application of plant breeding to develop crop varieties resistant to plant diseases and insects has employed the pragmatic approach, using simple recurrent selection *without* knowledge of the genetic basis of the resistance. It is not likely then that really costly and extensive pre-introduction biological control studies would be justified while the possibilities of obtaining outstanding successes are greatly delayed and even greatly reduced by the loss of potentially valuable genetic strains or species. This is especially true insofar as there is little evidence supporting the hypothesis that introduction of a complex of host-specific primary parasites could reasonably be expected to reduce the overall control effect below that of any single species introduced alone, although work of Hassell and May (1973) indicates that, theoretically, some such possibilities exist.

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Implementation and Economic Returns From the Systems Approach to Pest Management in Cotton

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ABSTRACT

A historical perspective of United States cotton insect management systems centered around the boll weevil is presented. The importance of using past technology and incorporating new technology into a total system approach is stressed. Methods are presented on the implementation of pilot pest management programs systems leading to large-scale expansion based on economic and environmental advantages.

The systems approach to the management of cotton insects in the United States is not a novel phenomenon. Before the late 1800's, cotton was produced with occasional damage and loss from insect pests. When the cotton boll weevil, *Anthonomus grandis* Boh., entered the United States via Texas in 1892; it rapidly spread across the south and southeast (Howard 1894). By the late 1920's this well-documented, devastating pest had extended its range eastward to the Atlantic seaboard and westward through the Rolling Plains of Texas. (Newsom and Brazzel 1968).

The destructive damage wrought by this pest induced early researchers to develop pest management systems to cope with it. The boll weevil became the focal point of these management systems. By 1916 the boll weevil was considered the principal pest of cotton in southern agriculture (Howard 1916). Because of the lack of effective insecticides, cultural practices were the basis of most recommended systems from the late 1890's through the early 1900's. Early planting, encouragement as much as possible of a early, rapid fruit set by seed selection and agronomic practices, early harvest and destruction of fall weevil populations by uprooting and burning cotton stalks after harvest to reduce boll weevils entering hibernation were components of this early system (Howard 1896, Hunter 1904). The philosophy of the system was based on the expedient production of an early cotton fruit set that would allow the crop to escape late season, high, damaging populations of boll weevils. Throughout the entire evolution of man's 84 year struggle against the boll weevil, the basic tenets of this earlier derived short-season management system are still valid and applicable. Cotton breeding programs in the early 1900's were directed toward the production of rapidly fruiting, short-season cotton varieties (Newell and Rosenfelds 1909, Hunter 1911). Searches were made with no success for a boll weevil resistant cotton variety. Again the emphasis was based on a rapid fruit set and, at all cost, the *escape* of late season damage was the goal.

Of the few insecticides known in the early 1900's the arsenicals proved to be most economical against the boll weevil (Newall and Barker 1908). In the insect control of that period, attention was focused on the use of calcium arsenate as the primary method to protect the cotton crop against the boll weevil. Although research in the areas of biological control continued, the then newly found arsenicals combined with cultural controls dominated boll weevil and other cotton insect control well into the late 1940's (Newsom and Brazzel 1968). Several recommended approaches for use of the arsenicals, and later the chlorinated hydrocarbons in the 1950's and 1960's are cited in the literature. These include applications for overwintered spring adults, scheduled season-long applications and fall applications directed at diapausing adults (Dunn 1964). The organophosphate insecticides were added to the chlorinated hydrocarbons in the late 1950's and early

1960's (Dunn 1964). Insecticides in general proved to be a ready-made easily, adapted approach to the solution of insect control in cotton production.

This general review of selected past boll weevil work is intended to add a bit of historical perspective and again point out that the individual components for an overall cotton pest management system were available. With the introduction of mechanical harvesting and harvest aid chemicals in the late 1950's and early 1960's, a method of terminating cotton before frost was available to further reduce the length of the growing season. It is difficult to determine the extent and belt-wide use of the various components in an overall pest management system.

Throughout the 1950's and 1960's, cotton insect control relied to a large extent on the wide-spread, season-long use of synthetic organic insecticides and calcium arsenate. The systems approach broke down as cotton varieties were bred for indeterminacy and high production. This method of cotton production is still being practiced in much of the south and southeast. This, essentially single component approach, began to break down as resistance to pesticides, first with the boll weevil to chlorinated hydrocarbons and then the tobacco budworm, *Heliothis virescens* Fabricius, developed a high degree of resistance to the major synthetic pesticides. Secondary pests, most commonly the cotton bollworm *Heliothis zea* Boddie, required further insecticidal control because of earlier insecticidal destruction of beneficial parasites and predators. The high cost of season-long insecticide control became economically prohibitive, particularly in the dryland cotton production regions of Texas and Oklahoma. The insect control system was out of balance and a return to the short-season management system was eminent.

Because of my familiarity with the history of Texas insect control and management systems, the remainder of this paper will be directed specifically toward Texas conditions. The current systems approach recommended in Texas today is not a great deal different than the short-season system promoted at the turn of the century. Fortunately recent strides have been made in the refinement and improvement of that earlier system. Short-season, rapidly fruiting, early maturing cottons were improved upon (L.S. Bird 1975, personal communication). Cotton varieties resistant to damaging insect species are being developed and incorporated into a short-season genetic background (P.L. Adkisson 1974, personal communication). Better timing of insecticides to minimize the secondary pest problems and impede the build-up of resistance are recommended. Alternatives in the agronomics of cotton production are being developed by narrowing row widths and enhancing earliness of fruit set, coupled with reduced nitrogen and water use in irrigated areas. (Walker, J.K. et al. 1976).

The statewide implementation of short-season cotton production as the basis for successful pest management in Texas has presented a special educational challenge. The fruits born by creative research will be left to spoil if programs are not developed to effectively incorporate new and proven technical developments into agricultural production. Because today's farmer, as in the past, is an independent, free thinking businessman, the advantages of a well designed insect management program must be clearly demonstrated in a broad based educational program.

As entomologists, we saw a need to increase the rate of adoption of integrated insect management. We asked ourselves why weren't farmers accepting even the most basic principles such as the most advantageous planting periods, the use of economic thresholds, thorough destruction of post harvest crop residues, etc? After much time spent analyzing this enigma, we came to the conclusion that we were greatly oversimplifying the problem. Putting ourselves in the farmer's shoes, we realized that a great deal of educational work would be required to overcome traditional practices and that growers basically viewed cotton insect control as a mystery. Farmers expressed their need for an entomological specialist to assist them in making difficult, key insect control decisions and aid them in designing an insect management program suited to their particular geographic regions.

Again, because of my familiarity with the Texas cotton pest management program, I will attempt to show by way of example how one might implement an integrated insect management program. Starting in 1972, by virtue of an APHIS-USDA grant, the 14 major cotton producing states received funding for the implementation of a pest management program. Based upon variances in insect pest problems, production techniques and geographic location in Texas, 4 areas were selected as pilot sites to begin the program (Lower Rio Grande Valley, South Texas, the Texas Blacklands and the Trans-Pecos). The organizational design of the Texas program is unique. County Extension entomologists, under the direction of a project leader, are located at each site. County entomologists are college graduates with field experience. The county entomologist resides in the area year around and has responsibilities for hiring and training sub-professionals (scouts) to inspect farmers cotton on

a weekly or bi-weekly basis for the occurrence of pest species and damage, the incidence of beneficial insects, the fruiting rate of the cotton, field moisture conditions etc. The scout delivers a Producer's Cotton Insect Report to the farmer. The county entomologist also receives a copy of the report. The report provides the aforementioned information plus the economic threshold levels for each key pest. The farmer can compare counts of pest numbers and damage with the economic threshold to determine the possible need for an insecticide application. The county entomologist is available to assist the farmer with his decision.

Scouting or field inspection is only one phase of the program. By using examples gained from past experience, the overall production of the cotton as it relates to insect management can be demonstrated. The pest management program heavily stresses early planting of an early maturing, rapidly fruiting, semi-determinate cotton variety. Such a variety and the method in which it is grown, i.e. with proper irrigation when used and fertilization, is the single, most important factor in managing the key cotton pests. The key cotton pests in order of seasonal occurrence are: (1) the cotton fleahopper *Pseudatomoscelis seriatus* (Reuter) (2) the cotton boll weevil and (3) the cotton bollworm/tobacco budworm complex. The selection of rapidly fruiting cottons condenses or shortens the period of susceptibility to insect attack. The cotton fleahopper, an early season pest, attacks the primordial buds and can be managed by careful field inspection and precise timing of insecticide applications when economic thresholds are passed. Every effort is made to keep early season insecticide applications to a minimum in order to preserve populations of parasites and predators which help suppress cotton bollworm populations. Boll weevil management involves a season-long strategy. This may require some early season insecticidal control of overwintered adults to allow a 2 to 3 week period for rapid fruit set. With favorable growing conditions these rapidly fruiting cottons will have the majority of their cotton produced on the plant before damaging, second generation boll weevil populations develop. The cotton is grown so as to escape damaging late-season insect populations. This escape character is also extremely important in dealing with the insecticide resistant tobacco budworm. Usually by July 10 in the Rio Grande Valley of Texas, the majority of the *Heliothis* population complex is the resistant *H. virescens*. If the cotton is grown properly, most of the bolls will be old enough to escape damage by the tobacco budworm. The incentive for early harvest is further enhanced to escape late-season weather problems that may hamper harvest. Finally, thorough destruction of crop residues after harvest is recommended to reduce the food supply of boll weevils going into diapause and prolong the host free period.

This is the general strategy employed in the Texas program. Year around educational programs are also conducted by the county entomologist. News releases during the production season alert other area farmers to insect problems. Close work with cotton and grain sorghum producer associations offer further means for program exposure.

The economic and environmental benefits of this approach have proven sound. A well designed economic evaluation of the 1973 and 1974 Texas Cotton Pest Management Programs demonstrated that net return to farmers participating in the pest management program increased over a similar group of non-participating producers by \$55.31, \$17.95 and \$30.59 in the Rio Grande Valley, Blacklands and Trans-Pecos program areas respectively, in 1973 (Frisbie et al. 1976). Similar profit increases were experienced in 1974. Increases in profit were a direct result of decrease in insecticide expenditures, increase in yield or both. An environmental evaluation revealed an estimated 82,000 pound reduction in pesticides applied to the 36,000 program acres during the two year period. (Frisbie et al. 1975. The 1974 Texas cotton pest management program annual report. Tx. Agr. Ext. Serv. Mimeo. Rpt).

The success and returns generated by the systems approach in the Texas Pest Management Program has resulted in statewide expansion of the program. Presently (1976) 17 cotton programs are operational in 36 counties in the Texas Statewide Pest Management Program. Grain sorghum pest management is included in these programs because of its key role in the cotton-grain sorghum agroecosystem.

In conclusion, let it be said that the well-planned systems approach historically has been the most well-founded and productive solution to the management of cotton pests. Presently, more than ever before, we have technical sophistication and educational input to make these systems work for Texas, the United States and the world.

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Systems Approach for Management of Rice Pests

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ABSTRACT

The control threshold of *Nephotettix cincticeps* Uhler (GRL), which transmits rice dwarf virus (RDV) to rice plants, is 0.1 adults/hill/day requiring heavy use of insecticides. Feasibility of population management of GRL was examined using an empirical lycosid-GRL system model having an equilibrium point. The effectiveness of lycosids and varietal resistance in controlling GRL, and the susceptibility of this system to insecticides were examined by simulation exercises. It is also suggested that abundant lycosids improves resilience of GRL population system.

Introduction

The panel convened in 1975 to discuss the problems on the integrated control of rice pests in Japan ranked the green rice leafhopper (hereafter GRL), *Nephotettix cincticeps* Uhler, as the number one key pest in southern Japan, followed by the brown planthopper, *Nilaparvata lugens* Stal, the rice stem borer, *Chilo suppressalis* Walker, the smaller brown planthopper, *Laodelphax striatellus* Fallen and heteropterous plant bugs in decreasing importance.

The damage caused by GRL is due to transmission of Rice Dwarf Virus (RDV) to rice plants. Direct damage inflicted on rice through its sucking behaviour is considered to be negligible, at least in southern Japan (Nakasuji and Nomura 1968, Kassai and Ozaki 1972). The control of hoppers, which include GRL, *N. lugens* and *L. striatellus*, involved 4-7 applications of insecticide during the 4 months of rice cultivation in 1969-71, in contrast to 1-2 applications in 1965.

In southern Japan, GRL has five generations and overwinters as mature nymphs (Kiritani et al. 1970). RDV disease is transmitted to rice plants by infective nymphs and adults. Since it is a persistent type of virus, individuals of GRL become infective through transovarial transmission and/or feeding acquisition of RDV from infected rice plants.

In the pre-War period, outbreaks of RDV occurred only sporadically in southern Japan lasting at most for 1-2 years. Since around 1955, this disease has become more prevalent as the result of an increase in the population density of GRL, and has inflicted considerable losses on rice yield (Nakasuji and Kiritani 1976).

The RDV epidemic is considered to have resulted from the following factors (Nakasuji and Kiritani 1976): (1) Increased cultivation of early sown rice which provides a favourable host for the 1st generation which otherwise develops on graminaceous weeds in the fallow paddy field. (2) Increase in the acreage of fallow paddy fields resulting from a decrease in the cultivation of such winter crops as wheat and barley. This provides overwintering nymphs of GRL with a large quantity of winter hosts. (3) Decimation of natural enemies of GRL by the use of such broad spectrum insecticides as BHC, parathion etc. to control *C. suppressalis*. Specifically, BHC was so toxic to spiders that even the granular formulation of BHC affected wolf spiders, *Lycosa pseudoannulata* Boes. Et Str., through the food-chain toxicity (Kiritani and Kawahara 1973). (4) The development of a high level of insecticide resistance to various kinds of organophosphates and carbamates. These conditions make GRL the principal target of the pest management system of rice pests in Japan.

Current Control Measures of GRL and RDV

With the extension of machine planting of rice seedlings, the application of granular insecticide at a rate of 50g/box (0.5 kg a.i./ha) to nursery boxes has been practiced. This method not only reduces the area treated by the insecticide by 1/300, but the amount of insecticide, as well as the frequency of application, can also be reduced to as much as ½ that of conventional control. In addition, the percentage of RDV infected hills can be reduced to 1/2-1/3 of that associated with the broadcasting of insecticide, while its effect on spiders can be kept to a minimum (Kiritani 1976).

Field experimentation has demonstrated that, when fallow paddy fields were ploughed on a large scale (e.g. 300 ha) during the winter, RDV epidemic could be suppressed almost completely within two years (Nakasuji and Kiritani 1976). This results from the destruction of hosts for overwintering nymphs that decimate the GRL population. Unfortunately, this cultural operation is not widely practiced, due to the labor shortage, and growers still depend largely on chemical control. The development of insecticide resistance, however, is imposing difficulties in controlling GRL by this method.

Control Threshold of RDV

The damage caused by RDV differs greatly depending on the developmental stage of rice plants. Early infection induces entire dwarfing of the rice plant, resulting in a total loss of rice yield. Consequently, control of RDV is composed of two different aspects. First, the prophylactic insecticide application against GRL to prevent the transmission of RDV to rice plants either in nurseries or immediately after transplanting. Secondly, the overall suppression of the population density of GRL in a given locality can be achieved by the management of GRL life system.

In applying prophylactic measures, it is important to know at an early stage the expected percentage of hills to be infected by RDV. An infection level of 15% of RDV infected hills, including early and late infection, is considered to be the level where some yield loss will result (Sugino 1975). The degree of RDV infection is determined by the following two factors: the population density of GRL and the percentage of RDV infected individuals.

Assuming random invasion of infective adults to the rice field, the control threshold, which is expressed in terms of the population density of GRL (per hill), can be determined by

$$A_T = 1 - \exp(-aNLV) \quad (1)$$

where A_T is the proportion of infected hills, a is the number of hills infected by an infective adult during its life span, N is the number of adults per hill that immigrated into the rice field, L is the mean longevity of adults under natural conditions and V is the proportion of RDV infective individuals (Kiritani and Nakasuji, unpublished).

By substituting the following values in Eq. 1, 0.15 for A_T (Sugino 1975), 1 for a (Ishii et al. 1970), 10 for L (Hokyo, personal communication), and 0.05, which is an average value for the 1st generation in Kochi (Nakasuji 1974), for V , we get $N=0.32$ adults/hill as the control threshold density of GRL.

Expressed in terms of the number of insects per hill per day over the invasion period (30 days), N can be written as

$$0.32 \times 10/30 = 0.1 \text{ adults/hill/day}$$

Such a low density as one adult per 10 hills (when $V=0.05$) imposes difficulty in controlling RDV infection, requiring heavy use of the insecticide.

Eq. (1) can be written as

$$NV = -\ln(1 - A_T)/aL = \text{constant}$$

Practically, it is difficult to manipulate V directly, because V is determined by the level of V in the previous generation, through the rate of transovarial transmission of RDV, and by the proportion of RDV infected hills in the paddy field. The latter depends in turn on the transmission/acquisition rates of RDV, the susceptibility of rice plants to RDV, the population density of GRL, etc.

Construction of Lycosa-GRL System Model

The management of GRL population can, however, be regarded as a long-range plan, and it is felt that the construction of a simulation model is essential in developing a management system for this species. In general, our approach has been to use life tables, from which our first model has been constructed (Kiritani et al. 1970). Since then, an RDV epidemiology model (Nakasuji and Kiritani 1972, Nakasuji et al. 1975), a life system model of GRL involving spiders (Sasaba et al. 1973, Sasaba and Kiritani 1975) and a predator-prey system model (Sasaba 1974, Kiritani and Kakiya 1975) have been developed. These system models have been constructed almost independently, on their own empirical data. Hence, their synthesis in one unified model remains to be achieved in the future. Of the models so far constructed, the predator-prey system model seems to be useful in the assessment of the effectiveness of predators on GRL populations, as well as for various simulation exercises.

Several spider species attack leafhoppers and planthoppers in paddy fields. Among them, *Lycosa pseudoannulata* is the most voracious and the predation by this species on hoppers made up to about 90% of the total cases of predation in the paddy field. Planthoppers usually appear in the diet of *Lycosa* late in the season but to a lesser extent compared with GRL (Kiritani et al. 1972, Kiritani and Kakiya 1975). The distribution of *Lycosa* and GRL in the paddy field is random (Kuno 1968, Kuno and Hokyo 1970, Kakiya and Kiritani 1976). In the analysis, the main emphasis was placed on finding an empirical way of modelling predator-prey system, starting with observed data.

The weekly disappearance rate (D) of *Lycosa*, which includes mortality, emigration and to a lesser extent loss of individual marks, is obtained from a mark-and-recapture analysis of *Lycosa* adults. The predation by *Lycosa* on GRL was also evaluated quantitatively by the 'sight count' method proposed by Kiritani et al. (1972). The disappearance rate (D) and the percentage (P) of GRL eaten by *Lycosa* per day are expressed by a set of multiple regressions as functions of densities of GRL (X) and of *Lycosa* (Y) (Kiritani and Kakiya 1975).

$$\log P = -0.84 \log X + 0.32 \log Y + 1.75 \quad (R^2 = 0.73) \quad (2')$$

$$\log D = -0.40 \log X + 0.34 \log Y - 0.11 \quad (R^2 = 0.98) \quad (3')$$

Eqs. (2) and (3) can be transformed as

$$\text{No. GRL eaten/day/hill} = 0.56X^{0.16} \cdot Y^{0.32} \quad (2')$$

$$\text{No. disappeared/week/hill} = 0.78X^{-0.40} \cdot Y^{1.34} \quad (3')$$

Here the powers of Y in Eqs. (2') and (3') denote the degree of interference between lycosid spiders.

In order to describe the predator-prey system, it is necessary to obtain the reproductive terms both for *Lycosa* and GRL. The reproduction components of this interaction system can be obtained empirically using the vector relationship illustrated in Fig. 1, where X_1 , Y_1 and X_4 , Y_4 are the values observed on successive censuses. The vectors X_1X_3 and Y_1Y_3 include respectively the increment of X and the deaths of GRL other than by the predation by *Lycosa* during one week and the increment of Y for the same period. The simplest expression of these vectors is to describe X_3/X_1 or Y_3/Y_1 as a function of X_1 and Y_1 . For the data pooled for the period of 1970-73, the following multiple regressions are derived (Sasaba 1974).

$$\log(X_3/X_1) = -0.40 \log X_1 - 0.03 \log Y_1 + 0.73 \quad (R^2 = 0.59) \quad (4)$$

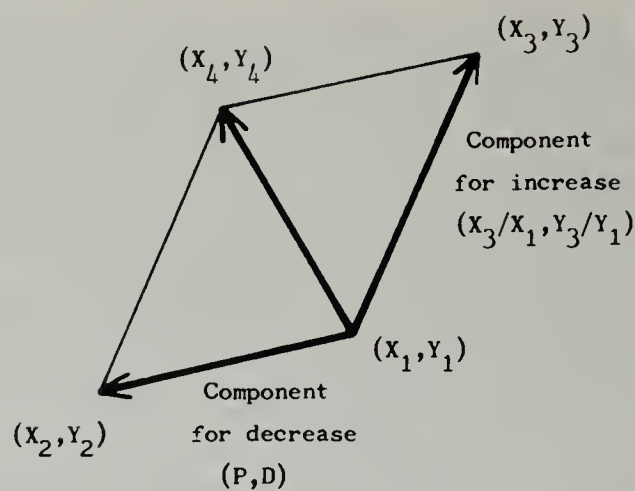
$$\log(Y_3/Y_1) = -0.06 \log X_1 - 0.10 \log Y_1 + 0.42 \quad (R^2 = 0.23) \quad (5)$$

or

$$X_3 = 5.37X_1^{0.60} \cdot Y_1^{-0.03} \quad (4')$$

$$Y_3 = 2.63X_1^{-0.06} \cdot Y_1^{0.90} \quad (5')$$

Eqs. (4') and (5') indicate that the values of X_3 and Y_3 are determined mainly by the density of their own species.



$$\begin{aligned}
 \begin{bmatrix} \text{NO. PREY} \\ \text{PREY} \end{bmatrix} &= \begin{bmatrix} \text{INITIAL NO. PREY} \\ \text{PREY} \end{bmatrix} + \begin{bmatrix} \text{NO. PREY RECRUITED} \\ \text{RECRUITED} \end{bmatrix} - \begin{bmatrix} \text{NO. PREY EATEN} \\ \text{EATEN} \end{bmatrix} \\
 \text{or} \quad X_4 &= X_1 + (X_3 - X_1) - (X_2 - X_1) \\
 \begin{bmatrix} \text{NO. PREDATORS} \\ \text{PREDATORS} \end{bmatrix} &= \begin{bmatrix} \text{INITIAL NO. PREDATORS} \\ \text{PREDATORS} \end{bmatrix} + \begin{bmatrix} \text{NO. PREDATORS RECRUITED} \\ \text{RECRUITED} \end{bmatrix} - \begin{bmatrix} \text{NO. PREDATORS DEAD} \\ \text{DEAD} \end{bmatrix} \\
 \text{or} \quad Y_4 &= Y_1 + (Y_3 - Y_1) - (Y_2 - Y_1)
 \end{aligned}$$

Fig. 1. — Vector relationship of *Lycosa*-GRL system. (X_1, Y_1) and (X_4, Y_4) are observed values on successive censuses, where X and Y refer number of GRL and *Lycosa* per m^2 , respectively.

Simulation

It is now possible to simulate the population changes of *Lycosa* and GRL using Eqs. (2) (3) (4) and (5). Matching between the computer output and the empirical data was examined using real data for the initial values of X and Y in running a simulation (Fig. 2). In general, the trajectories of calculated values traced relatively well those of empirical data. However, the calculated trajectories failed to mimic the variation of the observed data along the X axis. As evident from Fig. 2, there are two peaks in the GRL density each corresponding to the 2nd and the 3rd generations, but Eq. (4) does not incorporate such a time-dependent component.

The trajectories shown in Fig. 3 represent the sequential change of the two interacting populations at constant time intervals of one week (Sasaba 1974). The system achieves a stable node showing direct convergence with no looping from any point in the X-Y plane to the equilibrium point \bar{P} ($\bar{X}=15.5$, $\bar{Y}=18.5$). The shaded area represents the domain where densities of *Lycosa* and/or GRL become negative, in other words, where $D>1$ and/or $P>100$.

If the number of GRL at the equilibrium point corresponds to a *tolerable* level of the rice damage, then it would be desirable to have the system brought to that point. Once at the equilibrium point, the system would theoretically stay there and no further control would be needed, provided that there is no intervention by man, e.g. by harvesting, and no climatic disturbance, e.g. winter.

Conventional rice cultivation involves about 20 rice hills per m^2 . Given no perturbation from the outside, the total incidence of GRL (mature nymphs and adults) would be kept less than one insect per hill by *Lycosa*. However, this level is still too high for the successful control of RDV, i.e. 0.1 insects/hill when $V=0.05$.

From the practical point of view, it is interesting to examine the equilibrium density of GRL without *Lycosa*. In Eq. (4'), the term for *Lycosa*, $Y^{-0.03}$, takes values nearly equal to one with various possible values of Y. Hence, by transforming the equation to $X_{n+1} = 5.3X_n^{0.6}$, we can obtain the equilibrium density of GRL when *Lycosa* is presumed absent from the system. The solution for $X_{n+1}=X_n$ is 67GRL/ m^2 which is 4.3 times that of GRL under the presence of *Lycosa*. Consequently, the GRL outbreaks during the last 20 years can be explained through the destruction of spider populations by insecticides.

It is also interesting to examine the effective zone where *Lycosa* can be utilized to control GRL. The prey isoline, refers to the set of points at which the prey (or predator) population just maintains its density, can be drawn in the X-Y plane. The two isolines divide the co-ordinate system into four domains: *Lycosa*-increasing and hopper-increasing domain (A); *Lycosa*-increasing and

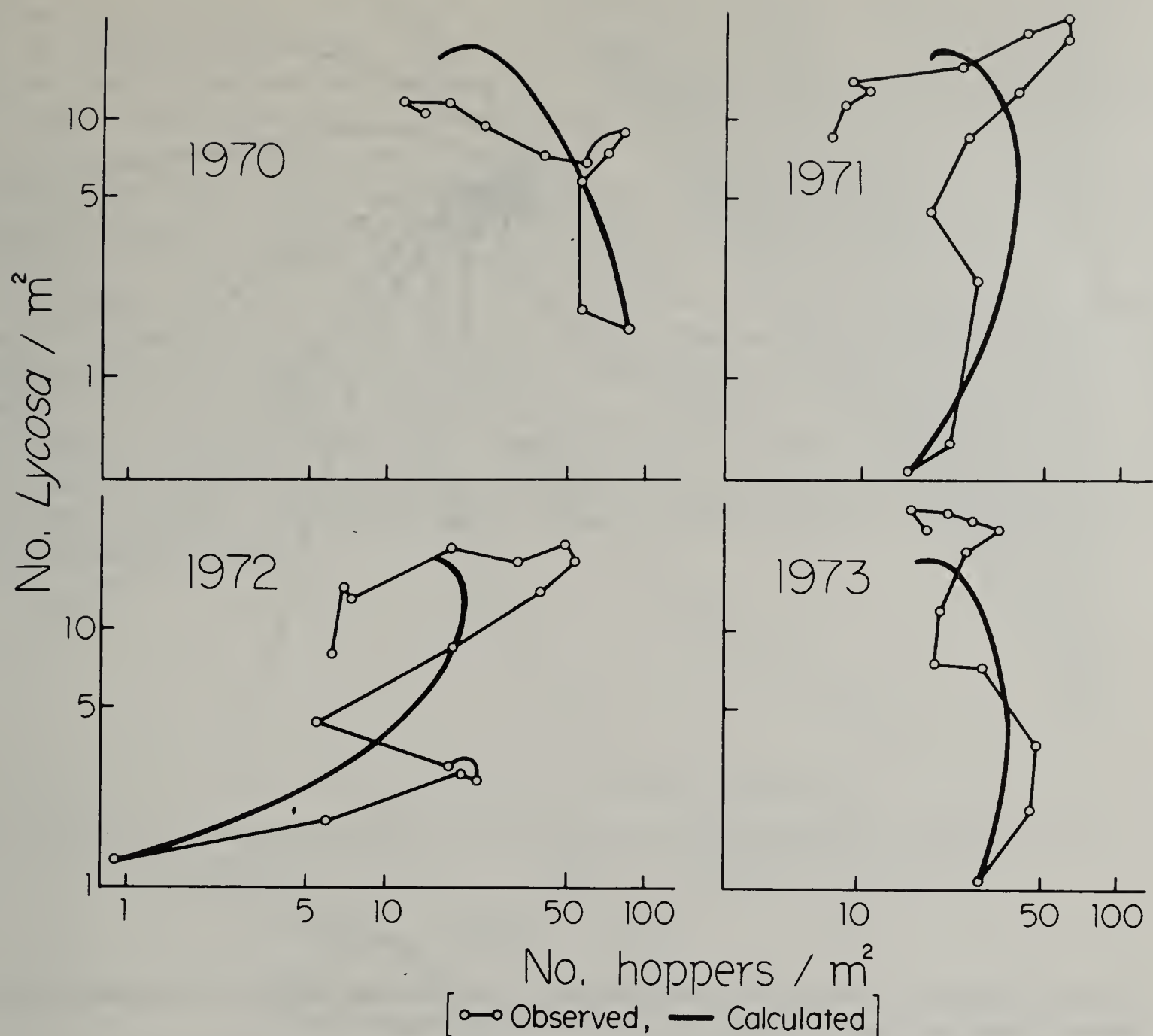


Fig. 2. —Matching between the computer output and the empirical data using real data for the initial values of X and Y in running a simulation (Kiritani and Sasaba, unpublished).

hopper-decreasing (B); *Lycosa*-decreasing and hopper-decreasing (C); and *Lycosa*-decreasing and hopper-increasing (D). It is suggested that effective biological control can only be expected in domain B, the reverse being the case with domain D (Kiritani and Sasaba, unpublished) (Fig. 4).

The susceptibility of this predator-prey system to insecticide was examined in the next simulation, assuming different effectiveness of the insecticide in killing predators and prey. When both populations are reduced by 50% every week, the equilibrium point is shifted from 18.5 in the control to 1.0 for *Lycosa* and from 15.5 to 6.3 for GRL. Simulation of BHC application, which is selectively toxic to *Lycosa* (Kawahara et al. 1971, Takahashi and Kiritani 1973), shows the resurgence of GRL due to the destruction of *Lycosa*; GRL increasing 2.5 times while *Lycosa* is decreased to 1/20 of those in the control (Kiritani and Sasaba, unpublished).

Finally the effectiveness of an integrated program, using a resistant variety and spiders in controlling GRL, was assessed by simulation using the interaction system (Kiritani and Sasaba, unpublished). The simulation suggests that a moderate degree of resistance to GRL, about 40% suppression of the increment (X_3/X_1 in Eq. (4)), is sufficient to control GRL. Contrary to *indica* types of rice, however, *japonica* type varieties which are grown in Japan seem to lack any resistant genes either to GRL or to RDV (Kiritani 1972). This simulation suggests that more effort should be made to breed resistant *japonica* varieties in the management of GRL population.

Concluding Remarks

Under natural conditions, it should be noted that neither the prey nor its predators reproduce during the winter and that both of them are exposed to winter mortality before they resume their

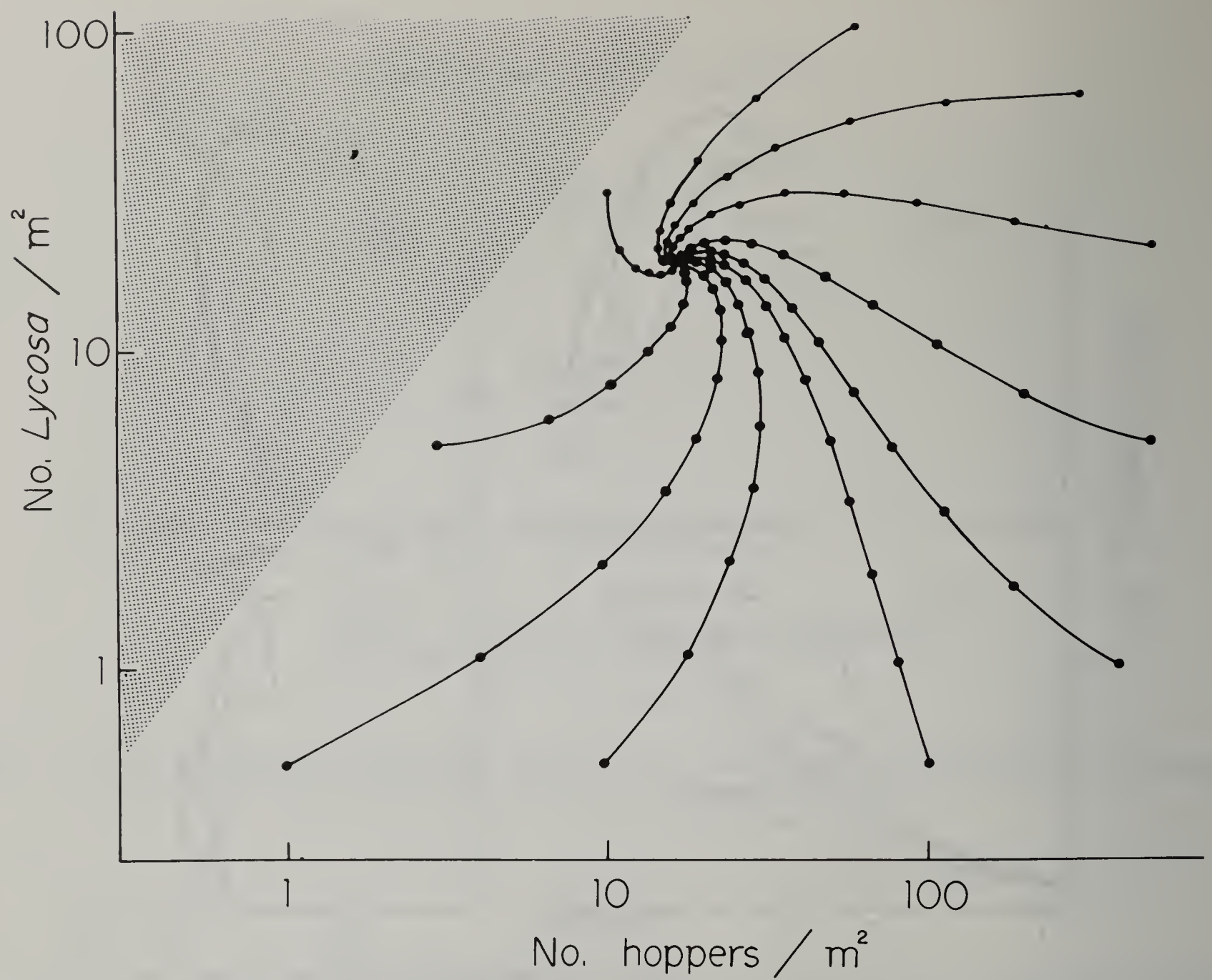


Fig. 3. –Sequential changes in densities of *Lycosa* and GRL at 7-day intervals predicted by the predator-prey system model. Shaded area denotes the zone where $D > 1$ or $P > 100$ (Sasaba 1974).

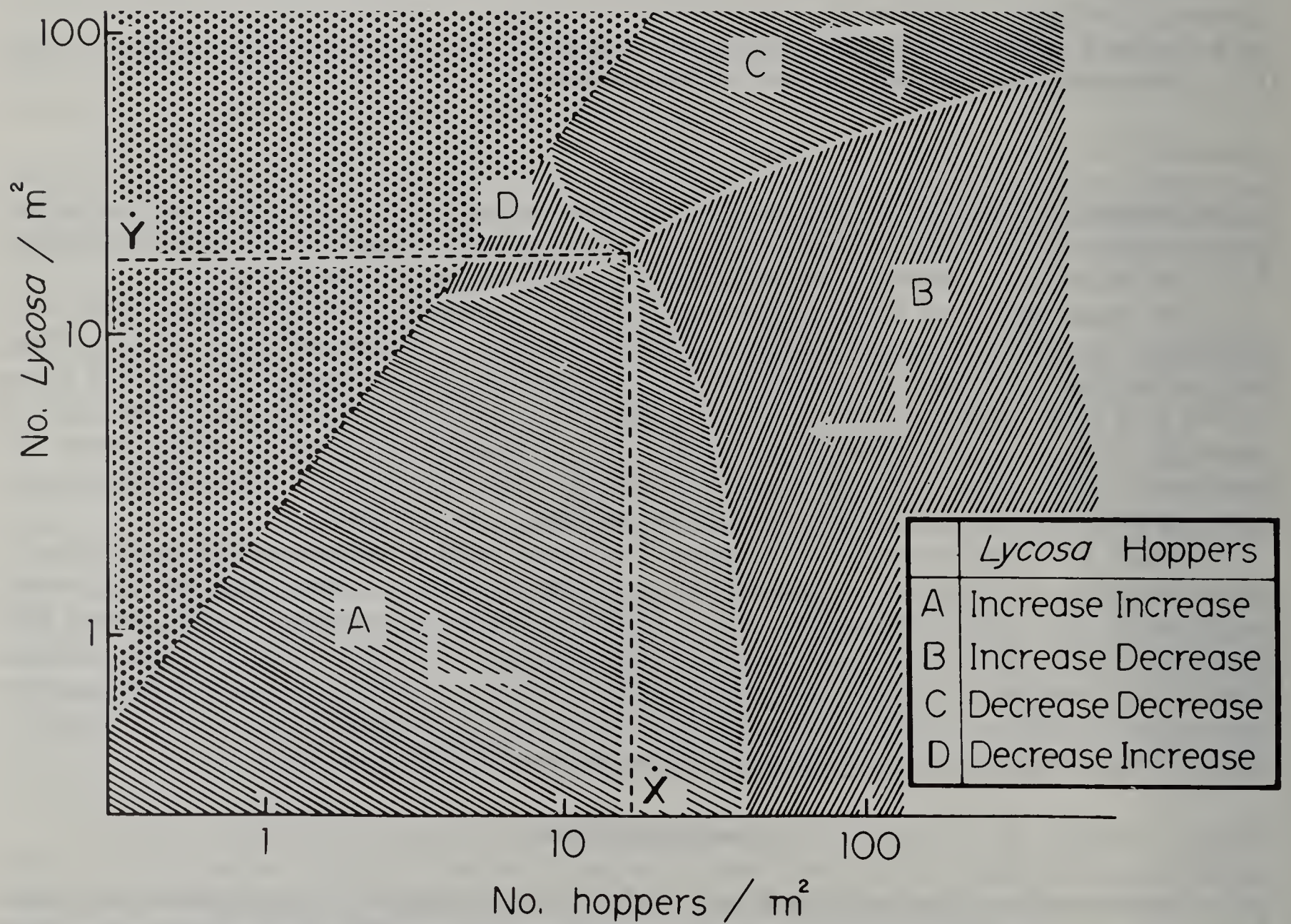


Fig. 4. –Showing the domain (B) where effective biological control of GRL by *Lycosa* can be expected (Kiritani and Sasaba, unpublished).

reproduction in the following spring. This means that the equilibrium point exists only theoretically and that the system starts each year from a combination of relatively low densities of both species. Another point which deserves to be mentioned is that the present system is constructed on the basis of empirical data. Consequently, the conclusions drawn only hold within the range of observed values and any extrapolation should be made with caution.

The life table study of GRL shows that two peaks appear in the mortality curve plotted against the population density of GRL (Kiritani et al. 1970). A series of mortality curves can be drawn between A and C in Fig. 5 with increasing density of *Lycosa*.

In the absence of *Lycosa*, GRL increases up to the point (E_H) through successive generations, or at most for three generations on a single crop of rice. The bimodal mortality curve produced by the presence of *Lycosa* intersects the fecundity curve at three points, E_L , R and E_H on the GRL reproduction curve. The salient point of this figure is that the GRL population becomes more resilient (Holling 1973) by lowering E_L (the equilibrium between GRL and *Lycosa*) and by increasing R (the escape threshold). This means that the higher the population density of *Lycosa*, the more feasible is the population management of GRL, since the GRL population is less likely to escape the predation pressure of *Lycosa*.

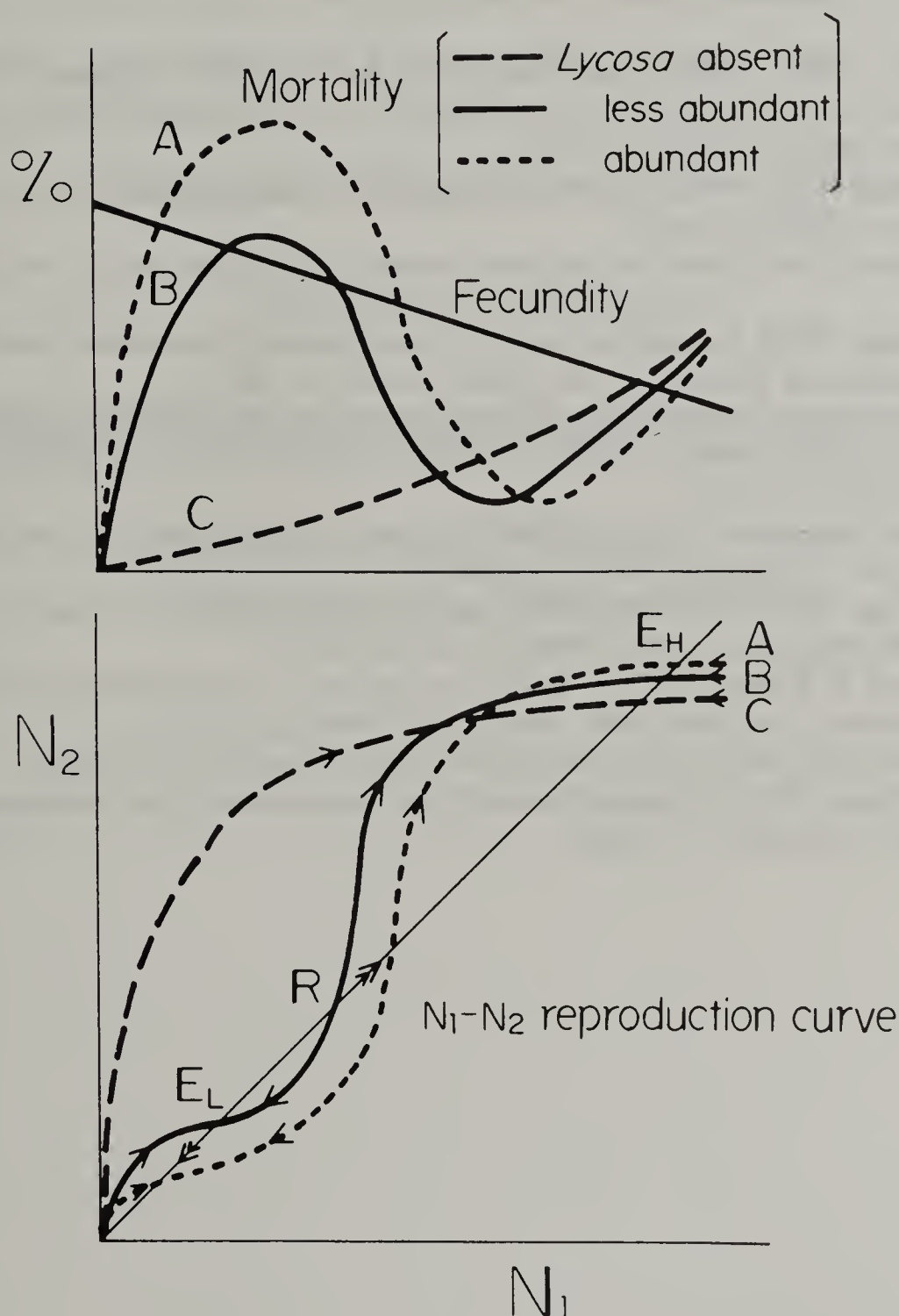


Fig. 5. —Hypothetical density-dependent changes in mortality and fecundity of GRL population with or without *Lycosa* (top), and the reproduction curves of GRL derived from the relationship between mortality and fecundity curves (bottom). Note that the resilience of the GRL population system is improved by the presence of abundant *Lycosa* as indicated by the double arrows on the 45° line.

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Section 10: Agricultural Entomology and Pest Management;

Section 8: Biological Control; and,

Section 5: Ecology.

Natural Factors Regulating Pest Populations

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The Potential for Manipulating Natural Control Factors for Plant Diseases

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ABSTRACT

Dynamic equilibrium between pathogens and their physico-biotic environment has long been manipulated by plant pathologists to control plant diseases. Biocontrol is now an integral part of the disease-control program, particularly for soilborne pathogens. Biocontrol of pathogens largely operates through resident or introduced antagonists by antibiosis and competition, with infrequent hyperparasitism. It emphasizes "nudging" antagonists by slight environmental changes, applying a "shock" treatment to specifically favor them, or inoculating them in large numbers to "swamp" the pathogen-favoring microbiota. Antagonists are passive and nonmobile, make accidental contact with the pathogen, and generally operate in mixed groups, rather than singly as in insect biocontrol. Pathogen-suppressive soils occur where a pathogen cannot establish, establishes but produces no disease, or its disease-producing ability declines with continued culture of the host. This suppressive microflora can be transferred successfully to conducive soils. Single antagonists may be effective on aerial parts if introduced before pathogen arrival on the host. Instances should be studied where the pathogen is present but causes no disease on susceptible hosts. Since pathogen inoculum comes from the host and/or soil, pathogen-free plant propagules and soil are indicated, supported by sanitation and biocontrol (including host resistance).

Biologists recognize a dynamic equilibrium between living things, their vast interacting network of ecological niches, and the physical environment. Plant pathologists have long manipulated the balance between pathogens and antagonists by altering the physical environment, usually without calling it biological control. Biocontrol is becoming an integral part of the disease-control program, particularly for soil-borne pathogens. Since entomologists may be unaware of the unique features of this type of control of plant pathogens, the main trends and concepts are outlined here, with examples of their application.

Microorganisms compete for nutrients, the most favorable sites, and oxygen, and are selected for tolerance of unfavorable conditions of carbon dioxide, ethylene, pH, water, and other microorganisms. They all secrete metabolic waste materials, some of which inhibit other microorganisms. A few of these antibiotics (e.g., penicillin, streptomycin) are utilized by man in medicine and agriculture. Some of these byproducts may stimulate certain microorganisms, causing increased growth or the formation of essential stages in their life cycles. Thus, metabolites from *Pseudomonas* bacteria are necessary for *Phytophthora cinnamomi* to produce zoospores, the principal root-infecting stage of this important pathogen in wet soil (Broadbent and Baker 1974). These stimulatory bacteria are destroyed by aerated steam treatment of soil at 60°C/30 minutes. Some microorganisms escape competition by parasitizing plants (producing disease) or other microorganisms (e.g., nematode-trapping fungi).

Environmental factors operate selectively on the crop, pathogen, and antagonists. Soil bacteria antagonistic to *Fusarium roseum* f. sp. *cerealis* 'Culmorum', cause of foot rot of wheat, cease growth in moderately dry soil of -10 to -15 bars water potential, but the pathogen can grow under quite dry

conditions (-75 to -85 bars). The wheat plant, drawing water from deep in the soil, continues to grow after the surface soil dries, but is increasingly attacked by *Fusarium* as the bacteria become inactive. This disease is controlled by seeding late and keeping soil fertility at low levels to produce smaller plants, and selecting varieties for high water efficiency, factors that delay soil-water depletion and prolong antagonism by the bacteria (Cook and Papendick 1970, Papendick and Cook 1974). *Fusarium* soilborne spores colonize clean bright straw when it is plowed under, increasing the pathogen population, but standing wheat stubble is colonized by saprophytes that prevent invasion by *Fusarium* when the straw is plowed under (Cook 1970). On the other hand, *Cephalosporium gramineum*, cause of a stripe disease of winter wheat, resists bacteria and fungi in moist soil, but is susceptible to *Penicillium* spp. when the soil becomes very dry (-150 to -210 bars) and the protective antibiotic of the pathogen is not produced (Bruehl and Lai 1968). Stripe disease is controlled by a single planting of spring wheat in the rotation.

Biological Balance and Plant Disease

The incredibly complex interactions between biotic and abiotic factors in soil provide an inconspicuous but dynamic biological balance that has tough resistance to change. To exist in such a complex association is to gain external strength and protection from the enhanced stability. Man plows up the mixed native vegetation, plants large areas of a single variety of an alien often susceptible crop and, by irrigating and applying fertilizer, produces an exceptionally favorable physical environment. Such abrupt violent alterations of the biological balance reduce or destroy the dynamic stability in the ecosystem.

The pathogen-suppressive state is the normal condition of biologically buffered equilibrium. Although parasitism appears to be normal for some microorganisms, pathogenism (the ability to produce disease) is uncommon. Health, rather than disease, is the normal state for life. It is doubtful whether agriculture ever would have developed if this were not true and if biocontrol of pathogens was not common. Biological control, in this interpretation, is the restoration of a disease-suppressing balance in nature. Biocontrol is working whenever man's disturbance of the environment permits it to do so. This need not require restoration of the original balance; a new one compatible with changed conditions may be satisfactory.

We know when a host-environment-pathogen-antagonist complex successfully produces a disease by the symptoms caused — a positive observation. When antagonists suppress the activity of the pathogen, however, there is no disease to see — a negative observation. Man only has time to cope with problems he recognizes, rarely to investigate those that give him no trouble. This is at the heart of the situation with biocontrol of plant pathogens. When it controls disease, the effect is apt to be attributed to an unfavorable physical environment or to excellent culture; when it fails, the notion of unreliability is strengthened. It is rather like the man who couldn't repair his roof while it was raining, and didn't need to when it wasn't.

It is a principle that plant disease is rarely controlled by a single procedure. Several factors, such as host resistance, proper cultivation, use of pathogen-free propagules and of fungicides, and biocontrol, usually are necessary for success. Man has tended to emphasize single-shot overkill procedures, and pathologists have developed a one-to-one syndrome. We seek *the* causal pathogen, have emphasized single-factor resistance and the gene-for-gene hypothesis, and have seen that entomologists seek *a* predator or parasite for biocontrol. A more enlightened viewpoint is to use biocontrol and other procedures in integrated control.

Comparison of Biocontrol of Plant Pathogens and Insects

Biocontrol of insects has been largely by predators and parasites that are actively mobile and seek their prey. Biological control of plant pathogens is through antibiosis, competition, and infrequent effective hyperparasitism by resident or introduced antagonists that are passive and nonmobile, make accidental contact with the pathogen, and generally operate in mixed groups, rather than singly as with insects. Entomologists have introduced a parasite or predator to a field and then analyzed the reasons for success or failure. Pathologists have studied individual pathogen-antagonist interactions, largely have depended on resident antagonists, and have attempted to increase their effectiveness through "nudging" by environmental manipulation, applying a "shock" treatment to specifically favor them, or inoculating them in such large numbers as to "swamp" the pathogen-

favoring microbiota. Pathologists have, therefore, made more use of pathogen-free propagules, sanitation, and breeding for resistance than have entomologists.

Suppressive and Conducive Soils

Soils naturally suppressive to pathogens are fairly common. They are recognized in the following situations:

a) A pathogen, although repeatedly introduced, does not become established or produce disease. *Fusarium oxysporum* f. sp. *pisi*, cause of wilt of peas, has been found in only two small areas in California, although many tons of infested seed have been sown, and resistant varieties are not required. However, when this soil is rendered nearly sterile by treatment, and the pathogen introduced, severe disease results. This indicates a functional biocontrol. This fungus causes severe damage to peas in the Palouse area of Washington. However, large populations of *F. roseum* f. sp. *cerealis* 'Culmorum' and the foot rot of wheat that it causes, are rare in this same soil (Baker and Cook 1974). When a massive quantity of a strain of *Rhizoctonia solani* that is damaging to wheat in the Eyre Peninsula of South Australia was introduced into a field in Adelaide and seeded with wheat, it temporarily caused severe plant damage, but disappeared from the soil in four months. A crucifer strain of that fungus is, however, commonly present in both soils (Baker et al. 1967). Such situations show that the pathogen-suppressive effect of soils is quite specific, and that it can be swamped briefly by large amounts of pathogen inoculum.

b) A pathogen is present in soil without producing disease, although it causes severe disease in similar soils nearby. In Queensland, Australia, *Phytophthora cinnamomi* is present in avocado groves without causing injury under 254 cm of rain in 7 months, and only limited injury under 140 cm of rain in 3 days. Treatment of the clay soil with steam at 100°C/30 minutes and inoculating with the pathogen makes it fully conducive and produces severe disease. However, the soil remains suppressive after treatment with aerated steam at 60°C/30 minutes, showing that the antagonism is due to thermal-tolerant spore-forming bacteria or actinomycetes (Broadbent and Baker 1974). The suppressive soils in Queensland orchards and rain forests (Broadbent and Baker 1975) and the drier Western Australia forests¹ have a high content of organic matter, high levels of calcium and ammonium nitrogen tied up in the organic cycle, adequate phosphate and magnesium levels, pH at about neutrality, and very high populations of microflora and -fauna. These features favor bacterial antagonists, particularly in the moist Queensland area. Very intensive cover-cropping and application of calcium, chicken manure, and super phosphate has protected a Queensland avocado grove from *P. cinnamomi* for nearly 40 years, while adjacent groves that did not follow these cultural practices were badly damaged. In some of the latter groves that have been replanted and the above culture applied for 3 years, the pathogen and root rot often have disappeared (Pegg 1976). The Queensland soil suppresses the formation of zoospores, the root-infecting stage in wet soil, by antagonizing sporangium-stimulating bacteria and by bacterial lysis of mycelium and spores. Soil in an avocado grove near San Diego, California, is even more lytic than the Queensland soil, but *Phytophthora* root rot is not prevented. This suggests that the suppression of bacterial stimulation of zoospore formation may be more important in biocontrol of *P. cinnamomi* than is bacterial lysis.

Soils suppressive to Panama disease of banana (caused by *Fusarium oxysporum* f. sp. *cubense*) are known in Central America (Stover 1962).

c) A pathogen is present in a soil and at first causes severe disease, but with continuous culture of the crop for several years, the losses diminish to insignificance. The common scab of potato, caused by *Streptomyces scabies*, declines in California and Washington soils after about 8 years of monoculture. The suppressiveness is destroyed by autoclaving, indicating that antagonists are involved. Transfer of 10% suppressive soil plus 1% alfalfa meal to non-treated conducive soil greatly reduced scab (Menzies 1959). This showed that it is possible to transfer a suppressive microflora *in toto* to a conducive soil. A green soybean cover crop plowed under between potato crops is decomposed by *Bacillus subtilis*, producing compounds toxic to *S. scabies* and preventing increase of scab (Weinhold and Bowman 1968). The take-all disease of wheat, caused by *Gaeumannomyces graminis* var. *tritici* also declines after 2-5 years of monoculture. The suppressiveness of the soil is

¹ Malajczuk, N. 1975. Interactions between *Phytophthora cinnamomi* Rands and roots of *Eucalyptus calophylla* R. Br. and *Eucalyptus marginata* Donn. ex. Sm. Ph.D. Thesis, Univ. Western Australia, Nedlands. 371 pp.

reduced by treatment with aerated steam at 40°C/30 minutes, and is eliminated by 60°C/30 minutes, indicating that the antagonists are not spore-forming bacteria or thermal-tolerant actinomycetes. It is possible to transfer suppressiveness to methyl bromide-treated conducive soil in the field by adding 0.5% suppressive soil (Shipton et al. 1973).

No one has yet isolated single antagonists that will produce the suppressive effect in nontreated soil against *P. cinnamomi* or *G. graminis* var. *tritici*, the only examples so studied. However, microorganisms individually antagonistic to pathogens in soil of near-sterility or in agar occur commonly in soil. Populations antagonistic to a given pathogen occur only in soils biologically suppressive to it, but individual antagonists may occur in many soils. It appears unlikely that a biologically suppressive natural soil can be explained in terms of a single antagonist, probably because of the complex interactions of microorganisms already described.

Modifying the Agricultural Balance

The biologically buffered equilibrium in a fertile cultivated soil makes it difficult to establish a microorganism, be it antagonist or pathogen. However, this can be done if the balance is drastically upset by some "shock" (e.g., chemical or heat treatment, or addition of some selective amendment), or by inoculating with antagonists in such numbers as to "swamp" the pathogen-favoring microbiota. That it is possible to establish a microorganism in natural soil is shown by the ability of root pathogens to spread to new areas. This illustrates the important point that the pathogen is selectively favored by having a highly specific substrate, the host, not available to other microorganisms. The inverse principle of selectively favoring antagonists, but not the pathogen, is fundamental in biological control. Thus, it appears at present that one should attempt mass transfer of total antagonistic populations when nontreated soil is involved, but one may use single microorganisms or small mixed groups of them when they are introduced into soil or onto plant tissue of near-sterility.

Heat may be used to differentially shift the microbial balance in soil. Treatment of soil with aerated steam (60°C/30 minutes) destroys pathogenic fungi, bacteria, nematodes, and nearly all viruses, as well as most weed seeds if the soil is moist for a few days before treatment (Baker 1962, 1971, Bollen 1969, Wuest et al. 1970). This treatment leaves a substantial portion of the saprophytic flora (sporeforming bacteria, some actinomycetes, *Penicillium* and *Aspergillus* spp.), many of which are antagonistic to pathogens and all of which prevent creation of a biological vacuum. Treatment of nursery soil in this way is widely used commercially to reduce the hazards from introduction of a pathogen to treated soil, and provides several other important advantages as well over the usual treatment at 100°C/30 minutes (Baker 1971). Suppressive soil so treated retains its suppressiveness to *Phytophthora cinnamomi* (Broadbent and Baker 1974) and *Rhizoctonia solani* (Olsen and Baker 1968), but not to *Gaeumannomyces graminis* var. *tritici* (Shipton et al. 1973).

In only one instance thus far studied, the take-all pathogen (*G. graminis* var. *tritici*) has it been found that the presence of the pathogen stimulates the increase of microorganisms antagonistic to it. This is a specific dynamic relationship, since dead or even avirulent mycelium of the pathogen does not produce the effect (Gerlagh 1968). Such an effect is to be expected when antagonists develop on the surface of the living mycelium, and in hyperparasitism. The rarity of this phenomenon in plant pathogens indicates that the concept of density dependency is "inoperative" there.

Some antagonists are known to be specific to the roots of certain plants. The resistance of monocots such as corn to *Phymatotrichum omnivorum*, cause of cotton root rot of the Southwest, is due to microorganisms selectively favored by roots of these plants. When grown in sterile soil free from antagonists, corn is susceptible to the pathogen (Black 1968, Eaton and Rigler 1946). Similarly, the take-all fungus of wheat does not attack roots of peas in the field, but in sterile soil it produces root rot (Zogg 1969). Root exudates, probably the most important factor in determining the quantity and type of rhizosphere microbiota (Rovira 1965), are subject to genetic control by the plant (Neal et al. 1970). The crop plant may thus be used in managing the rhizosphere microflora and thus root disease.

The pathogen may be starved by crop rotation, one of the oldest forms of biocontrol. Plowing under a mature barley crop before planting field beans in California and Washington decreases losses from *Fusarium solani* f. sp. *phaseoli* by decreasing the amount of available nitrogen in the tillage layer. Populations of the pathogen are not decreased by the barley. *Cephalosporium gramineum* is controlled in winter wheat in Washington by a single crop of spring wheat or peas (Bruehl and Lai 1968) because the fungus population is decreased. A crop of spring wheat in a winter-wheat schedule

controls snow molds (*Typhula idahoensis* and *Fusarium nivale*) by eliminating the host during favorable climatic conditions (Baker and Cook 1974).

Planting creeping legumes between rows of rubber trees in Malaya encourages luxuriant rhizomorph formation and fruiting by *Fomes lignosus*, cause of white root rot, in the litter. This rapidly depletes the food base of the pathogen, as well as favors antagonistic actinomycetes and other saprophytes. This is now the commercial control of this pathogen (Fox 1965).

Selective treatment of soil may eliminate or weaken the pathogen. The oakroot fungus (*Armillaria mellea*) is controlled after removal of infected trees in California orchards by soil treatment with carbon disulfide, which kills exposed mycelia and so weakens those in roots that they are killed by the antagonistic fungus, *Trichoderma viride*. The control results from an enduring shift in the soil microflora (Bliss 1951, Darley and Wilbur 1954). Aerated steam treatment of infected citrus trees at 33°C/7 days weakened the fungus, which was then killed by *Trichoderma* without injuring the trees. Carbon disulfide treatment also controlled Fusarium wilt (*F. oxysporum* f. sp. *asparagi*) of asparagus in California.

Growing *Crotalaria spectabilis* as a cover crop in peach orchards (McBeth and Taylor 1944) gave a 483% increase in fruit yield through controlling root-knot nematode (*Meloidogyne* spp.). Female larvae penetrated roots of this trap crop, and because giant cells were not formed there, the immobilized nematode starved or at least did not lay eggs.

Reduction of water stress on wheat by culture practices for control of Fusarium foot rot has already been mentioned. The biocontrol of root pathogens can be overwhelmed by man's activities. For example, waterlogging, for extended periods, of a suppressive soil infested with *Phytophthora cinnamomi* will temporarily destroy the suppression (Broadbent and Baker 1974). Growing wheat varieties of low water-efficiency, or the excessive application of nitrogenous fertilizer aggravates Fusarium foot rot (Cook and Papendick 1970, Papendick and Cook 1974).

Inoculation with Antagonists

Treated soil or freshly cut plant surfaces relatively free of competing microorganisms may be successfully inoculated with a single antagonist. *Fomes annosus* is thus effectively controlled in England by inoculating freshly cut pine stumps with spores of the low-grade but competitive pathogen, *Peniophora gigantea* (Rishbeth 1963). This treatment has been applied on 62,000 hectares of forest there. *Trichoderma viride* inoculated on pruning stubs with the pruning shears has controlled the silver leaf disease of plum (caused by *Stereum purpureum*) in France (Grosclaude et al. 1973). A spore suspension of *Fusarium lateritium* plus benomyl applied to fresh pruning wounds on apricot in South Australia (Carter and Price 1974) was effective in preventing infection by *Eutypa armeniacae*. The fungicide is effective against *Eutypa* (but not the *Fusarium*) and prevents infection until the *Fusarium* has established in the wood.

Inoculation of nearly sterile casing soil of commercial mushroom beds with *Pseudomonas multivorans* or *P. fluorescens* has controlled brown blotch of the caps caused by *P. tolaasii* through competition (Nair and Fahy 1976).

Corn seed inoculated with *Bacillus subtilis* or *Chaetomium globosum* and planted in Minnesota fields having a moderate inoculum density of *Fusarium roseum* f. sp. *cerealis* 'Graminearum' gave about as good control of seedling blight as captan or thiram seed treatment (Chang and Kommedahl 1968). It was found that *C. globosum* and *C. cochlioides*, which occurred naturally on Brazilian oat seeds, were the real basis of the "resistance" of these varieties to *Helminthosporium victoriae* when planted in the field (Tveit and Moore 1954).

When roots of stone fruit seedlings are dipped in an avirulent strain of the crown gall bacteria (*Agrobacterium tumefaciens*) and replanted in soil heavily infested with the virulent form, a high degree of control of crown gall is obtained (Moore 1975, New and Kerr 1972).

Increased germination and growth of seedlings often results from inoculation of seeds with saprophytic bacteria for still undetermined reasons. Some examples are: Pelleting carrot seed with *B. subtilis* before planting in nontreated field soil gave a 48% yield increase of marketable carrots. Oat seed dipped in a suspension of *B. subtilis* and field-sown gave a 40% increase in grain yield (Merriman et al. 1975).

The inoculation of the treated medium of propagative or seed beds with antagonists offers great promise because the antagonist occupies the site first, and possession is nine points of the law here, as

in court. The evidence so far suggests that the antagonists will be carried over with the transplant and protect the plant against subsequent infection.

Epilogue

Biological control thus adds another dimension to integrated control of plant diseases, but is not a single overriding procedure that replaces other methods. Since plant pathogens come from the host and/or soil (including organic matter in it and water that comes from it), it is important to use pathogen-free plant propagules and soil, and to support these desirable conditions with sanitation and biological control (including host resistance).

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Some Practical Implications of Recent Theoretical Studies of Host-Parasitoid Interactions

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ABSTRACT

Simple, analytical models of insect host-parasitoid interactions are valuable in pointing to many of the features of an interaction that influence stability and equilibrium levels. This paper focuses in particular on the importance of such factors as (1) the searching performance of the adult parasitoid population, (2) the survival of parasitoid progeny, (3) the rate of increase of the host population and (4) other mortalities affecting the host. In addition, the relationships between the parameters describing parasitoid search and the degree of polyphagy are discussed from the viewpoint of whether specific or polyphagous natural enemies are preferable for the control of pests of perennial crops.

Most definitions of biological control make some explicit statement about a desired reduction in pest equilibrium levels. This is the primary objective of biological control, to which we should add the secondary aim that the interaction remains sufficiently stable to prevent the host from sporadically re-emerging as a pest. A theoretical framework for biological control must, therefore, provide some insight into the features of an interaction that will lead to reduced equilibria and that will contribute to stability. In addition to this, there are some general strategic problems in biological control to which theoretical studies can provide insight. In particular, I will focus on the issue of whether specific or polyphagous natural enemies are preferable in biological control programmes.

Broadly speaking, there are two kinds of theoretical studies which may be relevant to biological control, reflecting a dichotomy that occurs throughout mathematical ecology. On the one hand, there are multi-parameter simulations based on detailed studies of a given system. Such models can hope to correspond sufficiently to a particular natural system to be a useful management tool (e.g. Conway et al. 1975, Conway 1976, Gilbert & Gutierrez 1974). At the other extreme are more abstract models that sacrifice detailed realism in an attempt to grasp at general principles. Such models have identified general relationships which have a marked affect on the outcome of an interaction. My major concern has been with such simple models and it is to these that this paper is devoted.

Equilibrium Levels

It requires no skilled theoretician to deduce that a population has an equilibrium level when its rate of increase is finely balanced by mortality or emigration. To extend this statement somewhat, let us consider one of the simplest of host-parasitoid models, that of Nicholson & Bailey (1935):

$$\begin{aligned}N_{t+1} &= F N_t \exp(-aP_t) \\ P_{t+1} &= N_t [1 - \exp(-aP_t)]\end{aligned}\tag{1}$$

where N_t , N_{t+1} and P_t , P_{t+1} are the populations of host and parasitoid respectively in successive generations. The equilibrium point (albeit an unstable one) in this model depends exclusively on the host rate of increase (F) and the searching efficiency of the adult parasitoids (a = 'area of discovery'). This dependence is shown graphically in Fig. 1.

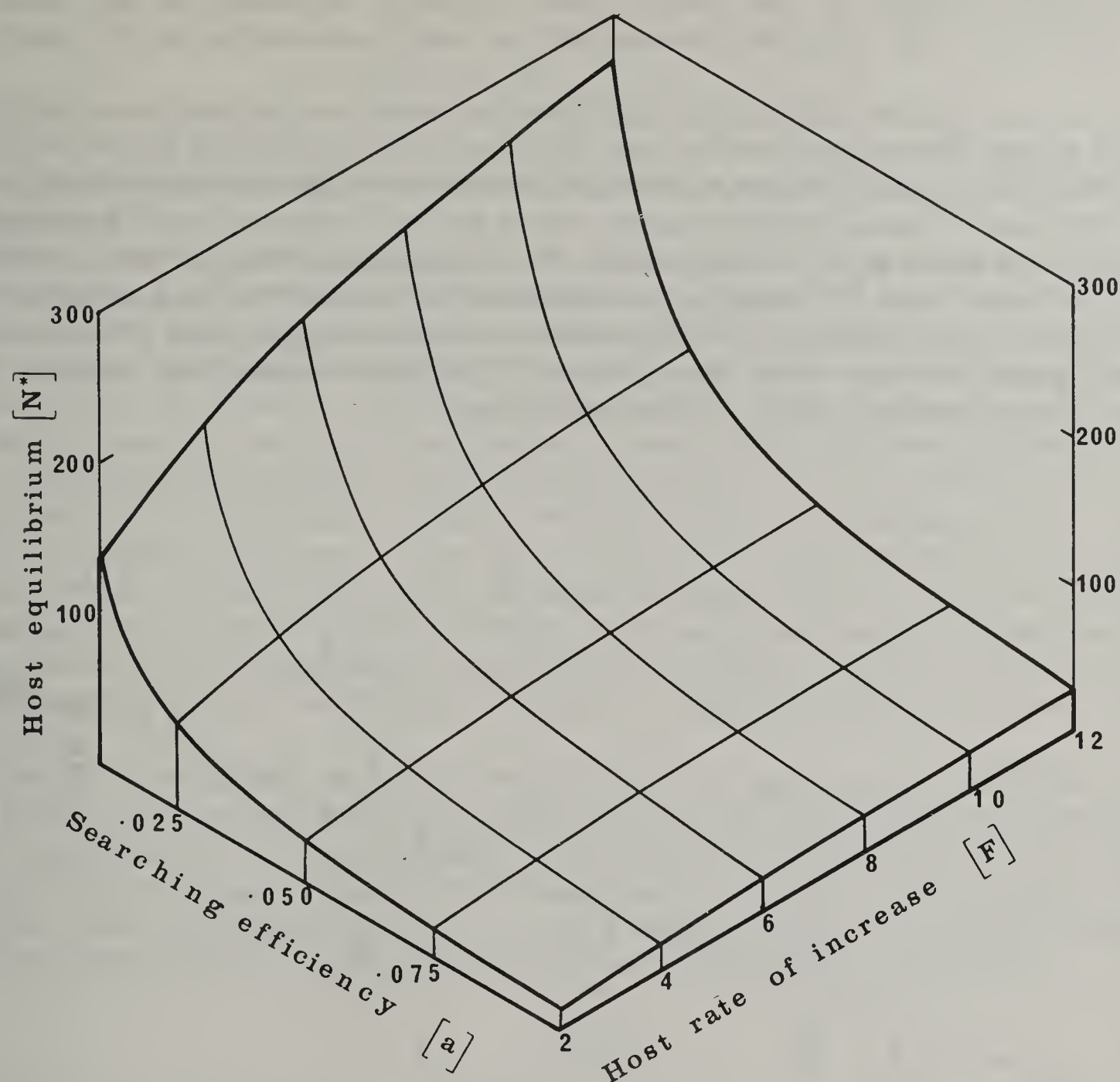


Fig. 1. —A three-dimensional surface showing the dependence of the equilibrium host population (N^*) on both parasitoid searching efficiency (a) and host rate of increase (F) from eqn. (1).

The overriding problems in relating this elegant picture to the practice of biological control are the over-simplified behaviour of the parasitoids and, perhaps more important, the total neglect of the many other hazards that affect both host and parasitoid populations. It is quite unrealistic, for example, to assume that a host population suffers no mortalities other than parasitism, and that the parasitoid population is itself free from mortality. Such factors may be crucially important in determining the final equilibrium levels (Hassell & Moran 1976). Fig. 1 should therefore be modified so that the F -axis becomes the 'effective' host rate of increase after all factors other than parasitism have been considered, and the a -axis becomes the overall performance of the parasitoid after due allowance for all factors limiting parasitoid search or the survival of parasitoid progeny. Clearly, without these modifications, the classical prey-predator and host-parasitoid models are of a simplicity that allows little direct extrapolation to the real world.

A most graphic example of how mortality factors other than parasitism (or the lack of them) can be crucial to the success of a biological control programme comes from the familiar studies of the winter moth (*Operophtera brumata* (L.)) in Wytham, England (Varley & Gradwell 1968, Varley et al. 1973) and in Nova Scotia, Canada (Embree 1965, 1966, 1971). There is a marked contrast between the population dynamics in the two locations. The winter moth in Wytham is often abundant but rarely defoliates the trees, whereas in Nova Scotia, after its initial accidental introduction, the winter moth spread rapidly and became a serious defoliator. A biological control programme was initiated in

Nova Scotia in 1954 in which two of the released parasitoids, the tachinid *Cyzenis albicans* (Fall.) and the ichneumonid *Agrypon flaveolatum* (Grav.) became established. Both introductions proved successful, with *Cyzenis* in particular being responsible for the decline in winter moth populations which are now maintained at very low equilibrium levels by the parasitoids. The situation in Wytham Wood is in marked contrast to this, since *Cyzenis* has almost no impact on the winter moth population and on the basis of this study would not have been recommended as a biological control agent.

This is an intriguing situation and fortunately one into which we can delve more deeply due to these detailed studies. They suggest that the most significant difference between the two winter moth populations lies in their pupal mortality. In Wytham, there is a very high winter moth pupal mortality (average of 72% over 17 years), probably mainly due to beetles and shrews, which is also markedly density dependent as shown in Fig. 2 (solid circles). The *Cyzenis* pupae, which are in the soil for some 10 months, also suffer a similar mortality, presumably at the hands of the same predators (Fig. 2, hollow circles). In contrast, Embree's (1965) studies in Nova Scotia suggest there to be a much lower winter moth pupal mortality there (approximately 35%), and without any apparent density dependence. This is represented in Fig. 2 by the broken line.

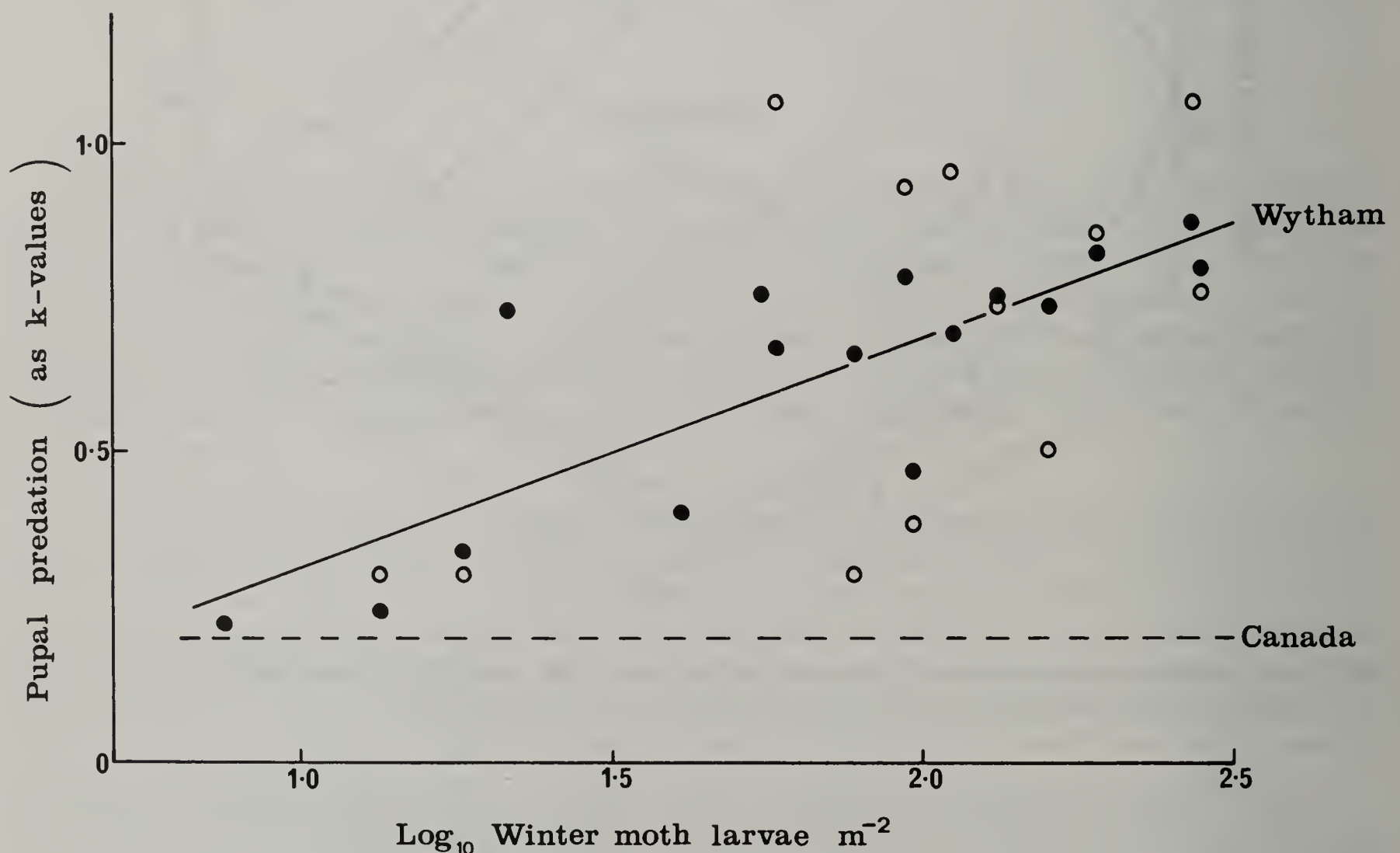


Fig. 2. —The relationships between winter moth pupal mortality ascribed to predation (expressed as k-values) and the density of winter moth larvae each year. (●) data from Wytham Wood (Varley & Gradwell 1968); (○) *Cyzenis* data from Wytham Wood (G.C. Varley, unpublished); (---) assumed winter moth and *Cyzenis* pupal mortality in Nova Scotia (Embree 1966). The solid line is the regression drawn through the Wytham data (○) ($y = 0.37x$; $p < 0.01$).

It is possible to show analytically just how important these pupal mortalities are to the winter moth equilibrium level. We commence with eqns. (1), but modify them to include the density dependent pupal 'predation' and other density independent mortalities known to occur. This now gives

$$\begin{aligned}
 N_{t+1} &= F\gamma_n(aN_t^{1-b})\exp(-aP_t) \\
 P_{t+1} &= \gamma_p(aN_t^{1-b}) [1 - \exp(-aP_t)]
 \end{aligned}
 \tag{2}$$

where aN_t^{1-b} is the density dependent pupal mortality of the form shown by the regression in Fig. 2, and γ_n and γ_p are the density independent mortalities acting on the host and parasitoid respectively (see Varley et al. (1973) for life table details).

The equilibrium winter moth population (N^*) is now obtained from the expression

$$A = a\gamma_p a = \frac{1}{N^*} \frac{[\ln(\gamma_n aF) - b \ln N^*]}{[(N^*)^{-b} - 1/(\gamma_n aF)]} \tag{3}$$

where $a\gamma_p a (=A)$ is the corrected parasitoid efficiency, just as $\gamma_n aF$ is the corrected, ‘effective’, host rate of increase.

Table 1 lists the values of the parameters in eqn. (3) that are appropriate to Wytham and to Nova Scotia, and Fig. 3 shows the resulting relationships between N^* and A for the two sites. These are in fact just two slices from the three-dimensional surface in Fig. 1, but now corresponding in some degree to a real situation. The position of each of these curves depends largely upon the host parameters: that for fecundity, mortality and the pupal ‘predation’ (which also equally affects the parasitoid). In contrast, the appropriate position *on* each curve for Wytham or Nova Scotia depends solely on the parasitoid parameters: that for searching efficiency (a) and mortality ($\gamma_p a$). Fixing these points from the data in Table 1, reveals dramatically different equilibrium levels, with that for Wytham being about ten times as great as in Nova Scotia. (The difference may well be further increased by the addition of the other introduced parasitoid (*Agrypon*) in Canada, which has not been included in this analysis.) This conclusion is not particularly sensitive to the exact parameter values assumed. Large changes in the values in Table 1 would be needed to move the curves, or the equilibrium points on them, sufficiently to reduce the considerable differences between Wytham and Nova Scotia.

Clearly, the additional pupal mortality in Wytham is in large part responsible for the much higher winter moth equilibrium level over that found in Nova Scotia. It has this affect by preventing *Cyzenis* from realising its true potential: it could be eliminated from Wytham with very little change in winter moth abundance (Hassell 1969). This analysis is really a cautionary tale. A seemingly unsuitable parasitoid (*Cyzenis* in Wytham) may prove spectacularly successful (*Cyzenis* in Nova Scotia) when liberated from quite independent factors operating within the system.

Stability

While the preceding model (eqn. (2)) helps us to focus on factors affecting equilibrium levels, it is deficient in an important respect: the host-parasitoid interaction itself is inherently unstable. Thus, the winter moth equilibrium in Nova Scotia, predicted from eqn. (3) without the density dependent

Table 1.—Values of parameters in eqn. (3) that are appropriate to Wytham (data from Varley et al. 1973) and Nova Scotia (Data from Embree 1965). (Asterisk denotes values for Nova Scotia that are assumed to be the same as in Wytham).

Parameter	Value for:	
	Wytham	Nova Scotia
b	0.37	0
F	75	75 *
$\gamma_n a$	0.06	0.016
$\gamma_p a$	0.38	0.63
a	0.075 m ²	0.075 m ² *
$A = a\gamma_p a$	0.028	0.047

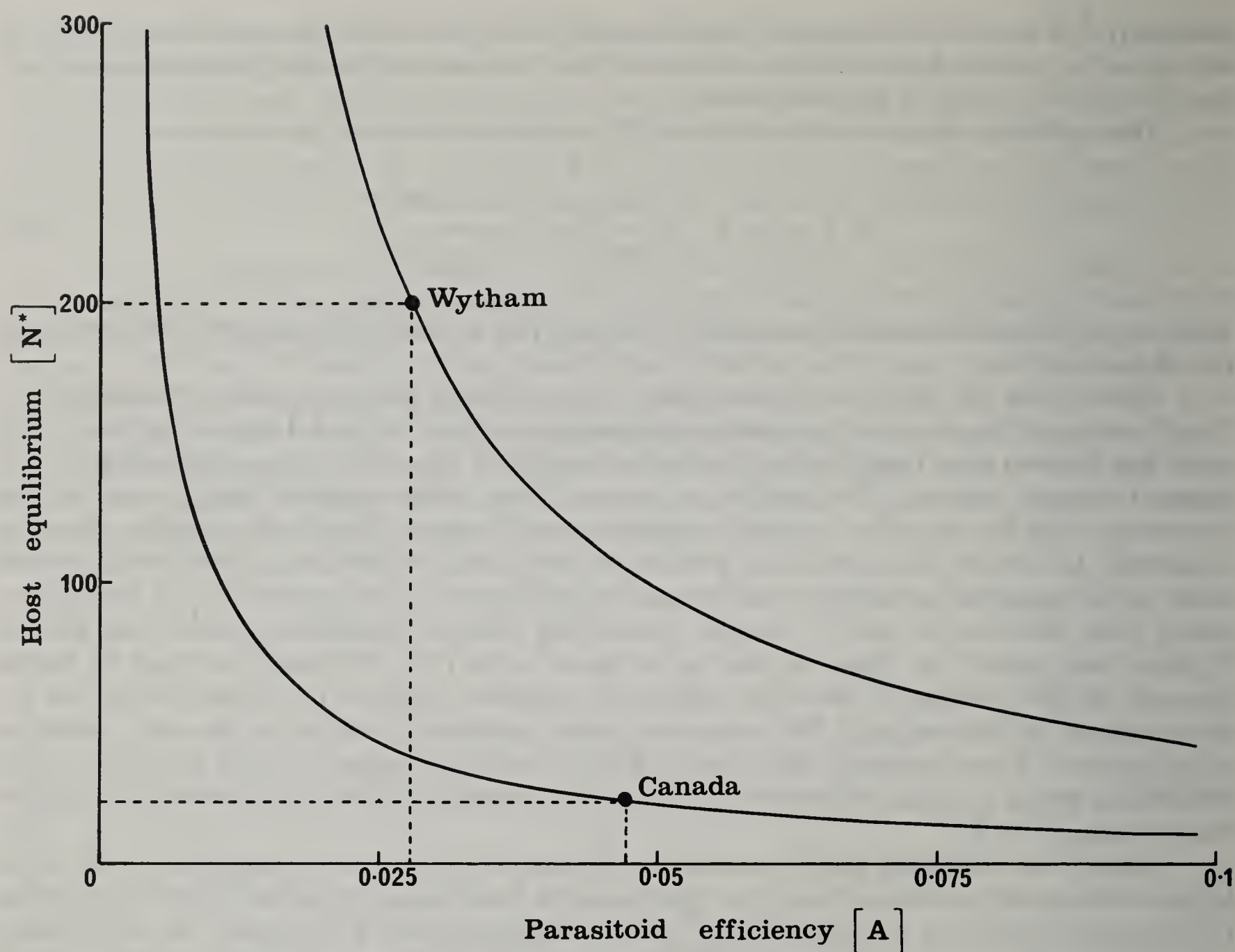


Fig. 3. —The relationship between host equilibrium (N^*) and the overall parasitoid efficiency, A (see eqn. 3). (0) represents the appropriate position on each curve corresponding to Wytham Wood and Nova Scotia. Parameter values from Table 1.

pupal mortality ($b = 0$), is an unstable one in which perturbations will lead to increasing oscillations. This is in marked contrast to the real world where true host-parasitoid equilibria resulting from biological control appear quite stable (e.g. Huffaker & Kennett 1966).

There is, of course, no *a priori* reason why successful biological control *should* lead to any change in the stability of the populations. (The temptation to think of very rare populations as more stable than abundant ones, just because their fluctuations are so small on an arithmetic scale, should be resisted.) What is certain in the context of biological control is that the factors responsible for stability will change. Prior to biological control, it is likely that resource limitation of the host population will be an important stabilising factor. After successful biological control, this can no longer be invoked, and we should now seek those properties of the host-parasitoid interaction itself that can contribute to stability.

Several recent studies have focused on the basic components of search by a parasitoid population, with a view to elucidating the effects of each response on the stability of an interaction (Hassell & May 1973, 1974, Murdoch & Oaten 1975, Hassell et al. 1976). Three responses affecting the outcome of parasitoid search have received particular attention.

The functional response to prey density

The functional response that is often associated with parasitoids and invertebrate predators is the type 2 response shown in Fig. 4a. Such a response can only be destabilising. There is a growing body of evidence, however, (Murdoch & Oaten 1975, Hassell et al. 1977) that sigmoid type 3 responses (as shown in Fig. 4b) may be just as typical for invertebrates. This is now a stabilising feature, provided that the average host densities fall within the density dependent part of the response (J in Fig. 4b).

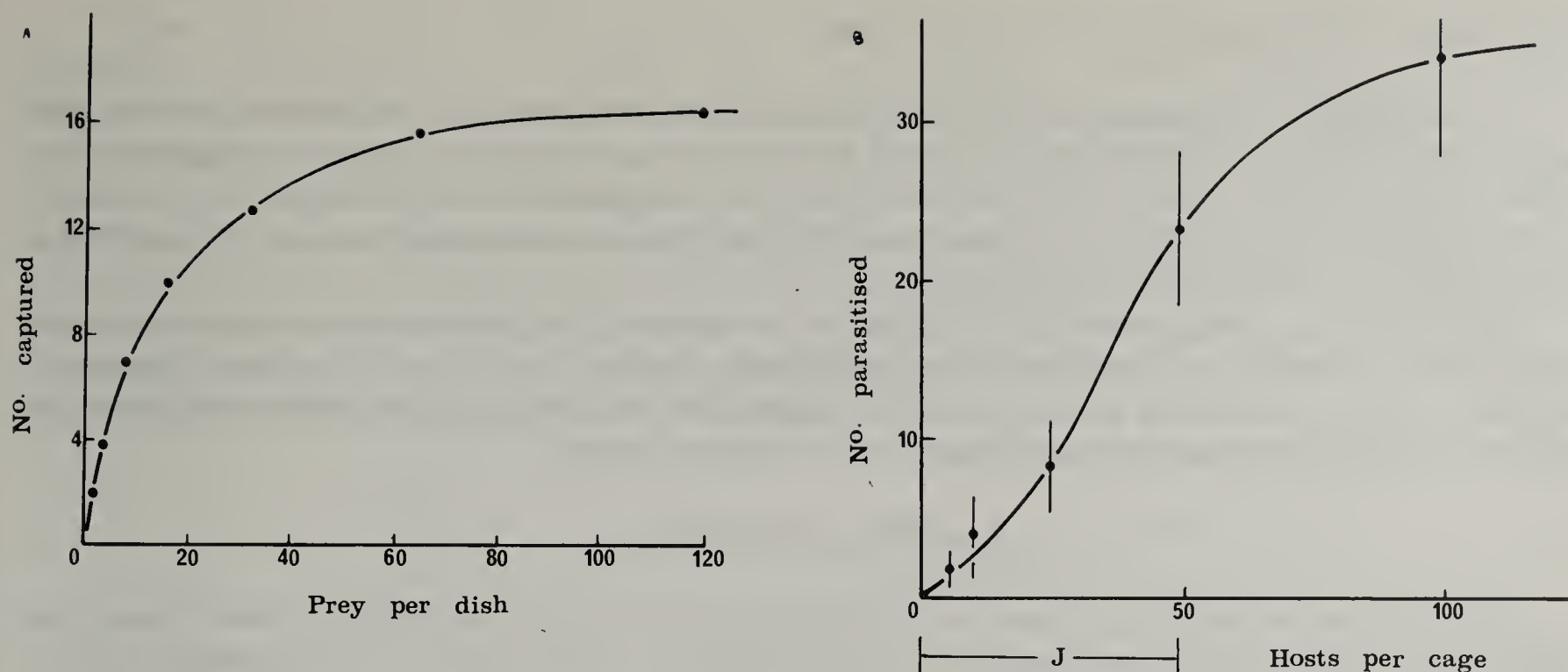


Fig. 4. —(a) A typical type 2 functional response shown by the coccinellid, *Harmonia axyridis* Pallas, feeding on the aphid *Aphis craccivora* Koch (after Mogi 1969).

(b) A sigmoid functional response shown by the braconid, *Aphidius uzbekistanicus* Luzhetskii, parasitising the aphid, *Hylopteroides humilis* (Walk.) (after Dransfield 1975). *J* represents the range of host densities over which the response is density dependent.

The response to the density of searching parasitoids

A decline in searching efficiency per individual as parasitoid density increases has been commonly observed from laboratory experiments (Hassell 1971). Inclusion of such interference in population models indicates that it can be a very powerful stabilizing mechanism. Indeed, if sufficiently strong, the host and parasitoid populations approach their equilibrium levels monotonically, rather than oscillatorily, as shown by the idealized biological control example in Fig. 5. Enthusiasm for this as a stabilizing mechanism in natural populations must, however, be tempered; it is as yet unclear the extent to which laboratory experiments exaggerate the effects of interference.

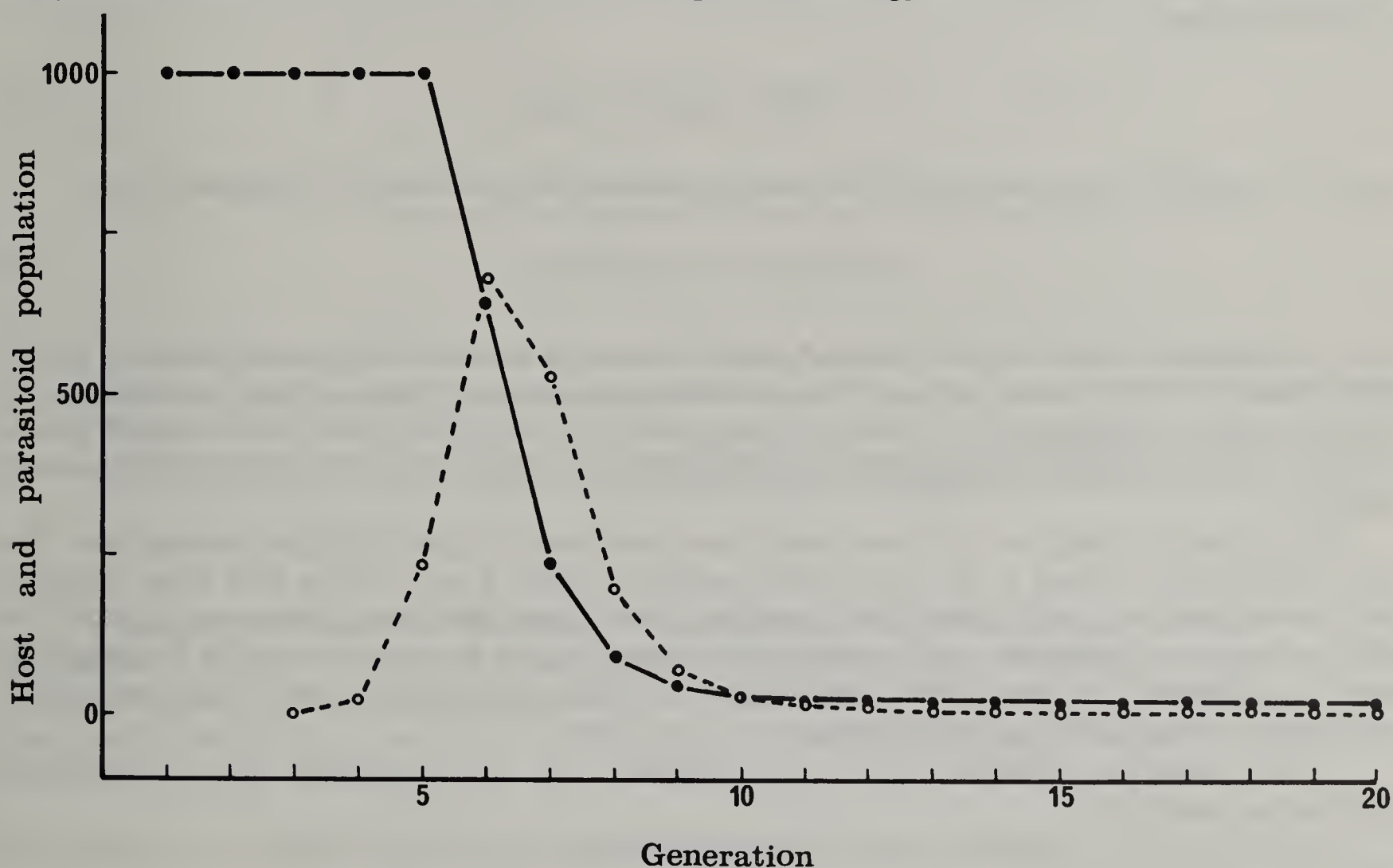


Fig. 5. —A simulation model illustrating how stabilising parasitoid behaviours (strong mutual interference) can lead to both populations monotonically approaching their equilibria (after Varley et al. (1973), in which model details are given).

A widespread and prudent strategy for a parasitoid (or predator) is to spend proportionately longer time searching in local areas of plentiful hosts. Several examples are given in Hassell & May (1974). On a population scale, this leads to aggregation of parasitoids in these areas. Dynamically, such behaviour is important as yet another (and probably the most widespread) means of stabilizing a host-parasitoid or prey-predator interaction.

The overriding message from such studies is that we must firmly discard any notion from early models that predation or parasitism is a destabilizing process. The mix of functional responses, interference and non-random search leading to aggregation will lead to rather stable interactions in which the classical prey-predator oscillations can be rapidly damped.

Specificity or Polyphagy

Most of the spectacular successes in classical biological control have been on pests of perennial standing crops such as fruit trees, and have involved specific or oligophagous natural enemies. In view of this, it is often assumed that relatively specific natural enemies (usually parasitoids) are better suited than widely polyphagous ones to maintain their hosts at a low equilibrium. It is supposed that a polyphagous natural enemy would not show a sufficient numerical relationship with just one of its range of host species to be as effective. In non-perennial crop plant systems, however, specific parasitoids have enjoyed much less success, and indeed Ehler & van den Bosch (1974) argue that polyphagous natural enemies are better suited as biological control agents in such systems where the concept of an equilibrium population is less appropriate.

In this section, the argument in favor of the use of specific parasitoid against pests of perennial standing crops is somewhat extended and made more precise. This is done by recourse to a combination of theory and biological intuition. The theory relates to the effects of various parameters of parasitoid search and the intuition to how these should be associated in specific natural enemies.

The searching characteristics in question are those which describe the potential searching efficiency (Q), the level of mutual interference (m) and the extent of parasitoid aggregation (μ). More precisely, Q is the searching efficiency (a in eqns. (1) and (2)), but in the absence of any interference, as in the expression

$$Q = (1/P_t) \ln(N_t/(N_t - N_a)) \quad (4)$$

where $P_t = 1$ and N_a is the total number of hosts parasitised; the parameter m is obtained from

$$m = (1n Q - 1n a) / (1n P_t) \quad (5)$$

where a is the searching efficiency when P_t parasitoids are searching; thirdly μ , which need not be further defined here, is some measure of parasitoid aggregation in regions of high host density. As discussed earlier, the significance of these to a host-parasitoid interaction is that high values of Q tend to lead to low equilibrium populations, while significant m - and μ -values will confer the necessary stability.

With these in mind, we can now make some sweepingly general biological observations. The most fundamental of these is the notion that parasitoids with a very narrow host range are more likely to respond to specific cues from a particular host species than are polyphagous species. The several examples of relatively specific parasitoids making use of host pheromones in locating their hosts (e.g. Mitchell & Mau 1971, Sternlicht 1973) are appropriate here. There are several consequences of such efficient host location.

1. The searching efficiency (Q) for a particular host species will be higher than for a polyphagous parasitoid.

2. Local areas of high host density will be more efficiently discovered, leading to a higher value of the aggregation index, μ .

3. More efficient aggregation (μ) will lead to more frequent parasitoid encounters and hence perhaps to more mutual interference (m).

These effects suggest several expected correlations between m , Q and μ and the degree of polyphagy. Unfortunately, the available data is very restricted, coming chiefly from laboratory experiments in which m and Q are measured for parasitoids whose host range is roughly known. Two relationships between the parameters, however, stand out. Figure 6a shows a positive correlation between the values of m and Q . It suggests that the more active and mobile species — those with a higher value of Q — are likely to encounter each other more often, so leading to greater interference. The more interesting relationship from the stance of this discussion, however, is that in Fig. 6b where the value of Q tends to decline as the range of acceptable host species increases. In other words, a restricted host range seems to be correlated with a high searching efficiency. A fuller account of these relationships between parameters is given in Hassell (1976).

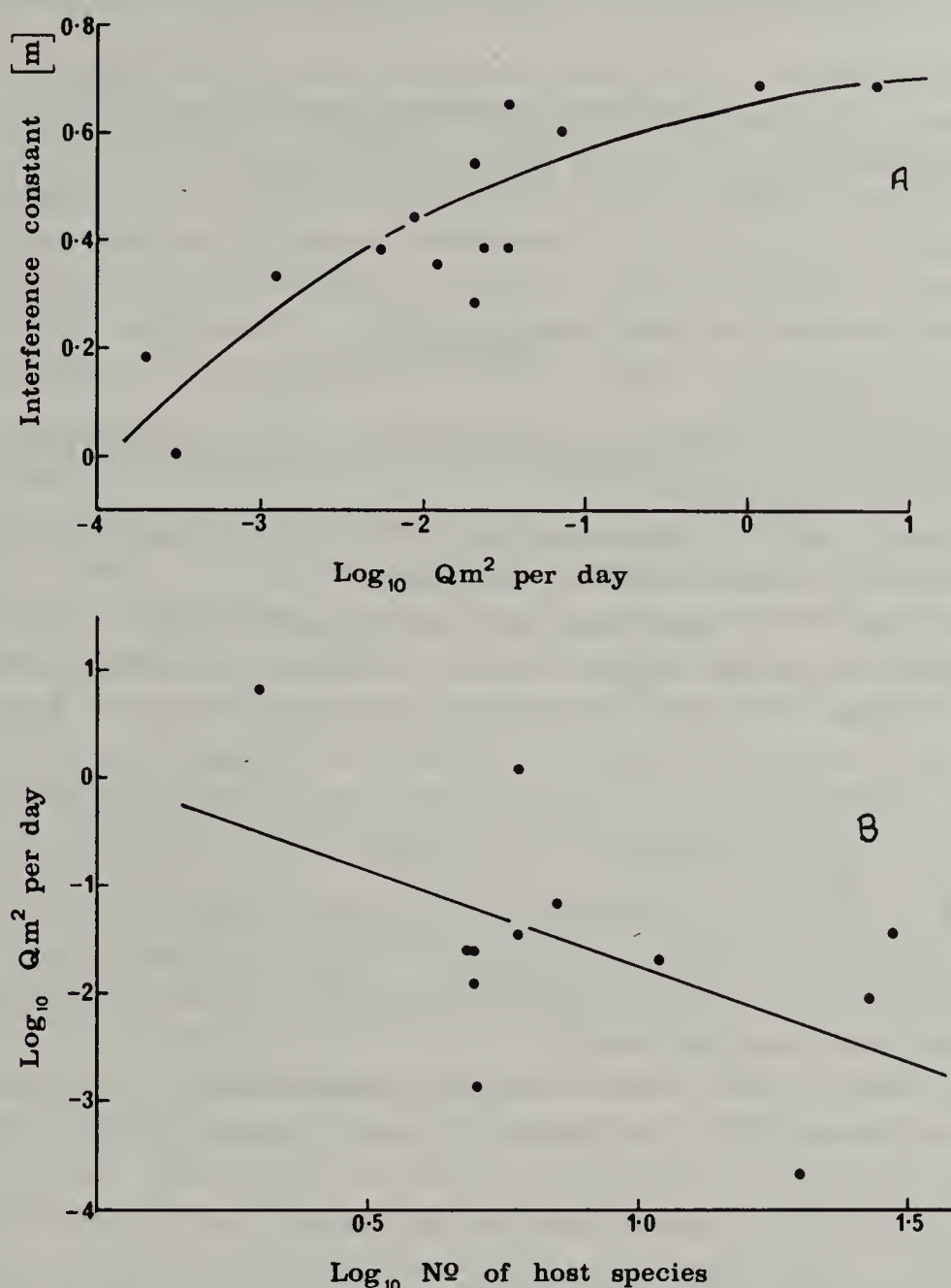


Fig. 6. —(a) The relationship between the degree of mutual interference (m) and searching efficiency (Q) for a variety of parasitoids and predators under laboratory conditions. The curve is fitted by eye and further details are given in Hassell (1976).

(b) The relationship between Q and the known range of host species accepted. Bracketed points indicate a quesstimated value for host or prey range. (Fitted line from the regression: $y = 0.004 - 1.75x$; $p \approx 0.05$).

It appears, therefore, that specificity in natural enemies is associated both with high values of Q (leading to low equilibrium populations) and with high values of m and μ (leading to stability). Thus by choosing the more specific parasitoids for introduction in biological control programmes, workers have been drawing from a subset of available species that have the potential at least to provide very low and stable host equilibria.

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Natural Control Factors Operating in Some European Forest Insect Populations

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Introduction

Natural control is considered as that force which keeps all living creatures in a state of balance (Van den Bosch and Messenger 1973). This state of balance is not only a rather relative, but also a complex phenomenon; it may ideally studied when one of the involved components is either highly dynamic or stable. Forest insects are well suited to elaborate on the concept of natural control: since

1. they show characteristic large amplitude fluctuations in their numbers
2. the forest environment represents a most stable ecosystem relative to the insects generation time
3. host trees of forest insects are generally widely distributed and occur often in very different ecosystems.

Two very different aspects are involved in the natural control of insect numbers. The physical-chemical or abiotic environment provides the variable constraints under which biological evolution takes place. Since the abiotic environment itself does not respond to the evolution of organisms, it determines the changes in numbers. In contrast the biotic environment, which includes mates, food, competitors and antagonists, induces reciprocal adaptation by density dependent interaction. These latter processes regulate insect numbers about an average level of abundance (Wilbert 1970, Varley et al. 1973).

In the course of nearly 200 years of forest management in Europe much qualitative and quantitative information on major forest pests has been accumulated. This paper discusses the impact and the interactions of the abiotic and biotic environments respectively on the fluctuations of some forest defoliators in central and northern Europe. I shall not deal with bark beetles as they never played the role in European forestry that they do in North America (Vité 1976).

The Impact of the Abiotic Environment on Insect Numbers

The biological implications of the abiotic environment depend on its variation in time and space, but also on the size of the organism and its mobility.

On a global scale, seasonal temperature and rainfall pattern are the major factors which are responsible for the distribution of organisms in space. Plants and insects become adapted by the process of natural selection to the combinations of these two factors. Most favourable combinations of temperature and rainfall can be inferred from the distribution and extension of outbreak areas of insect pests relative to the distribution area of the pest and the host plant. Eidmann (1949) visualized the distribution area of a species schematically as a circular space beyond which the species cannot thrive whereas the living conditions become more favourable from the periphery towards the center, the proper outbreak area. The noctuid *Panolis flammea* Schiff., the pine beauty, reflects this idea quite well. The outbreak area with frequent defoliation damage lies in continental areas of low annual precipitation of 400-600 mm and July temperatures between 17°C-19°C. Other species do not follow

this conception at all. Outbreaks of the oak tortricid, *Tortrix viridana* L., occur throughout its distribution area.

Topography, soil characteristics and depth of the groundwater level superimpose regional or local variations on the large scale pattern of population dynamics. Topography determines cold air drainage and temperature inversion which inflicts 100% egg mortality upon *Oporinia autumnata* Bkh. populations, a geometrid which defoliates vast areas of mountain birch in Scandinavia (Tenow 1975). Outbreaks of the pine insects on the diluvial plains of Northern Germany occur within the western subatlantic as well as in the eastern subcontinental climatic region, but each species prefers characteristic sites on the plains south of the front-moraines (Kruel 1955).

But greatest variation of insect numbers is induced by the variability of weather itself. We may distinguish between the climatic oscillation which may last for several decades and the yearly variability of weather parameters at short term up to 4 years.

Insects react regionally by an increased frequency of outbreaks or even more drastically by a corresponding shift in the outbreak area. Thus, *Porthetria monacha* L. defoliated during the recent climatic optimum in 1947-1948 spruce forests in the Bavarian Alps at 1100 m a.s.l., i.e. at altitudes 300 m higher than ever observed (Pschorn-Walcher 1954). The longterm pupal records of pine insects from various German forest areas (Cramer 1962, Schwerdtfeger 1941, Varley 1949), reveal that population changes do not seem to be random, densities increase for several subsequent years until defoliation occurs. Cramer (1962) analyzed the weather conditions which released the outbreaks. In general dry and warm weather during the young larval instar for two or three subsequent generations were sufficient; however the temperature requirements of the various species differ characteristically in time and amount. The pine beauty needs the least, *Dendrolimus pini* L., a lasiocampid moth, the largest amount of heat to reach outbreak densities. Consequently outbreaks of the different species occurred repeatedly in an orderly sequence. The pupae of the pine looper are regularly found at Schwetzingen (Cramer 1962), nevertheless there was only one outbreak recorded during the 110 year observation period. This secular event occurred when precipitation during the period of moth flight, i.e., in May and June, was extremely low for three consecutive years.

In contrast to these pine insects the larch bud moth, *Zeiraphera diniana* Guenée, presents an example where standard weather conditions favour population increase. This situation is a prerequisite for the cyclic fluctuation whereby the subalpine larch stands are defoliated at 9 year-intervals. Cool and rainy spring weather restricts defoliation to the regionally warmest sites whereas positive temperature deviations lead to widespread defoliation, including usually suboptimal sites in northwest exposure (Baltensweiler 1964, 1977). However, in other mountaneous areas of Europe, where *Z. diniana* lives on Scotch pine and Norway spruce, outbreaks occur at irregular intervals. Since the beginning of this century, two periods of outbreaks can be distinguished; the first from 1915-1935 and the second from 1955-1972. The releasing weather conditions appear to be more complex as those favouring the pine insects: warm spring seasons must be followed by cool summers and cold winters (Baltensweiler 1966, Day 1976).

In summary, abiotic factors impose a specific but consistent pattern of outbreak probability and thus delimit areas of fastest population growth. This pattern of optimum areas is best recognisable in the first year of visible defoliation when no mass-emigration on a local scale, induced by defoliation, has to be taken into account. A spatial model of such optimum areas is exemplified by the larch bud moth in the European Alps and the lodgepole needle miner in the Rocky Mountains, both species induce tree damage within a limited altitudinal zone along the mountain slopes.

The Biotic Environment

The plant/insect relationship may be considered in terms of food, shelter and transport (Southwood 1973). This discussion deals with the interaction of the plant as food and insect density only. The limited quantity of food determines the ultimate density level of any phytophagous insect whereas the variable food quality influences development and survival of the insect at any density level. Food quality may change regardless of density due to intrinsic or extrinsic causes, but also in a density dependent manner due to the insects feeding impact.

It is surprising that the role of food quality in forest insect dynamics is rather poorly understood (Bombosch 1972). However, recent investigations on the nutritional properties of oak leaves and needles of Norway spruce revealed that their nutritional value is restricted in time and quality. The optimum feeding period for the winter moth has to be conceived as a narrow gap

delimited at the outset of the season by lack of food and ended by chemical deterioration of the aging oakleaves due to an increasing content of tannins which inhibits larval growth (Feeny 1970). Lunderstädt (1973) established that the protein content of Norway spruce needles, which serve as food for the Diprionid *Gilpinia hercyniae*, can be utilized only partly and to a variable degree by the sawfly larvae, although it is present in surplus quantities (Bombosch 1975).

Various hypotheses have been proposed to explain insect outbreaks and vertebrate cycles by variations in the nutritional quality of host plants (Schwenke 1962, Van der Linde and Voûte 1967, Otto 1970, Kimmins 1971, Schultz 1969), but opinions are still controversial. In most instances warm and dry weather is considered to trigger the change in food quality. This appears to relate White's (1969) "stress index" in that plant stress is correlated with an increased amount of nitrogen available for the insect.

The process of coincidence between flushing of the host tree and the emergence of the first larval instar is recognized as a key factor in the population dynamics of the winter moth (Valery et al. 1973) and the oak tortricid (Schütte 1957). Optimum establishment of *T. viridana* is linked with a very specific stage of bud development, therefore maximum survival may shift from early sprouting oak trees to late flushing trees in different years. Consequently population density varies the least in oak stands containing equal proportions of flushing types, whereas density fluctuates strongly in oak stands consisting of either type only. However, recent investigations by Schwerdtfeger (1971) on outbreak and non-outbreak oak tortricid-populations reveal that the coincidence process alone does not sufficiently account for the discrepancies in the fluctuation type. Schwerdtfeger (1971) postulated that polyphagous, plurivoltine parasitoids fail to follow the increasing pest population in subsequent years of improved coincidence conditions because the increased second parasitoid generation over-exploits the alternate host-populations. Therefore, an incipient outbreak cannot be stopped by the parasitoids and may persist due to the low vagility of the oak tortricid moth (Gregor 1957) for several years. In contrast, in non-outbreak areas with regularly poor coincidence parasitoids are efficient enough to regulate host populations at low densities. The life system of the winter moth exhibits very similar aspects. The combination of determining and regulating key-factors, i.e. coincidence and pupal predation and larval parasitism respectively, derived from lifetable studies in England (Varley et al. 1973) proved to be equally effective in the atlantic provinces of Canada, to where *Operophtora* was introduced by accident (Embree 1971).

By experience it is known that the various pest species represent at maximum density quite different hazards to the survival of the host tree. Besides the fact that deciduous trees are intrinsically much less vulnerable to defoliation than conifers, regeneration capacity and/or survival depends on time and intensity of defoliation (Schwerdtfeger 1970). Great efforts have been devoted to establish those critical density which threaten the future of the stands (Richter 1960), but comprehensive research on the interaction among the various pest species and/or the host tree is still very scanty.

The array of pest species on pine, exhibiting selective feeding habits on old and new foliage, would provide an excellent opportunity to study their variable impact on the host. It is conceivable that negative feedback mechanisms are detected similar to what has been found with *Pristiphora abietina* Christ. (Ohnesorge 1962) and *Zeiraphera diniana* (Vaclena 1975). In both cases a change in physical or olfactory properties of the attacked plant induces a change in the egg laying behaviour and subsequent dispersal of the adult female to unimpaired plants. This mechanism provides relief to the host before irreparable damage has been inflicted. A most drastic interaction results from complete defoliation of the larch tree by *Z. diniana*. The larch tree refoliates immediately afterwards but increased fibre content and reduced protein content in the following year causes heavy mortality to the early larval instars (Benz 1974). This density induced antibiosis selects for a slow developing, heterozygous ecotype during the following 3-4 generations until full recovery of the tree allows again the survival of a dark, fast developing ecotype (Baltensweiler et al. 1977, Day and Baltensweiler 1974). Thus, the bud moth cycle may be conceived as being brought about by directional selection for two fitness types triggered by self induced change in food quality in a continuously favorable climate. The very narrow range of maximum densities (274.1 ± 1.2 larvae/kg larch foliage) reached at regular time intervals of 8.64 ± 0.29 years indicates that this upper density limit is determined by the quantity of food, whereas the spectacular 30,000-fold change in density within 4 generations exemplifies the speed of genetic revolution (Mayr 1963). The persistence of the cycle since 1850 confirms that other possible disturbing influences are of minimum effectiveness.

The prevalence of the resistant bud moth ecotype in the non-outbreak area suggests the permanent impact of a stress situation the nature of which is not yet analyzed. But the transitory,

statistically significant increase of dark ecotypes in this endemic population, observed in 1973 at the culmination of the cycle in the Alps, reflects:

1. the phenomenon of long range dispersal of subalpine populations and
2. the phenomenon of a strong directional selection for the heterozygous ecotype.

Recent investigations on oligophagous bud moth populations in England indicate the operation of disruptive selection (Baltensweiler et al. 1977, Day 1976).

The fluctuation of the pine looper has been studied for 24 years in Holland where it never causes any defoliation damage (Klomp 1973). It was demonstrated that during the first 14 years variations in density were due mainly to juvenile mortality but an outburst of parasitism lowered the mean density level by a factor 10. Klomp does not exclude that a change in genetic composition might also be involved. Another example of conspicuous ecotype variability, obviously related to population dynamics, emerges from the studies on *Acantholyda nemoralis* Thoms., a Pamphilid species on Scotch pine in Poland (Burzynski 1961, Koehler 1956, Sliwa 1968). These are just two examples which would prove worthwhile for further studies with regard to evolutionary ecology.

Concluding Remarks

European forest management promoted inadvertently a great stimulus to the study of population dynamics of insects. Extensive plantings of pines as far back as the beginning of the 19th century favoured large scale outbreaks. The systematic addition of a hardwood understory reduced the recurrence of calamities considerably (Lüdge 1971, Klimetzek 1972). Thus stand composition is of prime importance for a species becoming a pest. However, *Choristoneura fumiana* and *Zeiraphera diniana* are examples of defoliators which influence stand composition of natural forests (Blais 1974, Baltensweiler 1975). Fortunately there are only a few insects which exhibit such a dominant role on the forest ecosystem. It seems desirable to classify insects according to their evolved ecological niche, but since the interaction of natural control factors is in most cases not yet fully understood, such a classification appears still premature. Although a complete understanding of the population dynamics of an insect is not an absolutely necessary prerequisite for a successful forest pest management, comprehensive longterm studies on selected insect species in different environments and/or exhibiting different types of fluctuation provide the base for intelligent management.

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Natural Factors Operating in the Population Dynamics of *Heliothis zea* in North Carolina

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“Nature” is the most comprehensive term in man’s vocabulary. It includes “the entire material universe and its phenomena” (Funk and Wagnalls’ Standard College Dictionary, 1968 edition). Yet in studying the population dynamics of species, scientists commonly restrict their concept of “natural factors” (and unfortunately their studies) to factors other than man’s actions. This restriction may be justified as a point of departure but is untenable if a truly holistic understanding of populations of agricultural pests is to be developed.

The noctuid *Heliothis zea* (Boddie) evolved in the Americas and, during the last few hundred years, much of its biomass has been generated within, or flowed through, agricultural systems from Canada to Argentina. The cultural practices which maintain these systems adjust the environmental framework within which various demes exist and strongly influence their spatial and temporal patterns. Thus we include the cultural practices essential to crop production among the “natural control” factors operating in the population dynamics of the corn earworm, *H. zea*.

Our objective is to improve the description of spatial and temporal patterns of *H. zea* and to explain both the persistence and changes in these patterns. Our research target is the general population over a wide area rather than any single component of it on one of its many hosts. This holistic approach is essential if our objective is to be accomplished, because population potentials at each local focus (i.e., a particular field of a host) are largely determined by patterns of invading moths originating from other, and at times distant, sources. Additionally, the various mortalities reducing these local potentials are influenced by intercommunity factors such as movement of natural enemies. Thus, only through a broad study of the general population is it possible to include the effects of

The *H. zea* life system extends into, and is a part of, many divergent communities, both managed (cultivated) and unmanaged (uncultivated). Its complexity can be analysed and understood only through a modeling effort. However, our objective is not to construct a mathematical model, per se, but to use modeling procedures to further our understanding. These procedures involve literature analysis and research as well as symbolic and mathematical representations of conceived subsystems, which are continually reviewed and adjusted to accommodate new and more accurate knowledge and insights. HELSIM-2, an improved version of HELSIM-1 (Stinner et al. 1974a), and MOTHZV-2 (Hartstack et al. 1976) were developed within the context of the Cooperative Regional Project S-59: “Ecology and management of *Heliothis* species on cotton, corn, soybeans, and other host plants.” HELSIM and MOTHZV are wide-area population models most applicable to agroecosystems in North Carolina and Texas, respectively. As to be expected, both models share a similar conceptual framework and include submodels of the more obviously significant ecological processes. However, there are some differences in how these processes are modeled and these differences will be discussed in the section on model components.

Basically, HELSIM has been constructed to present the production flow of life stages on four principal host plants as depicted symbolically in Fig. 1. The principal processes intrinsic to *H. zea*, which mediate the numbers flow from stage to stage, are appropriately indicated in Figure 2. The next step was to include the effects of specific environmental factors on the rate of flow from stage

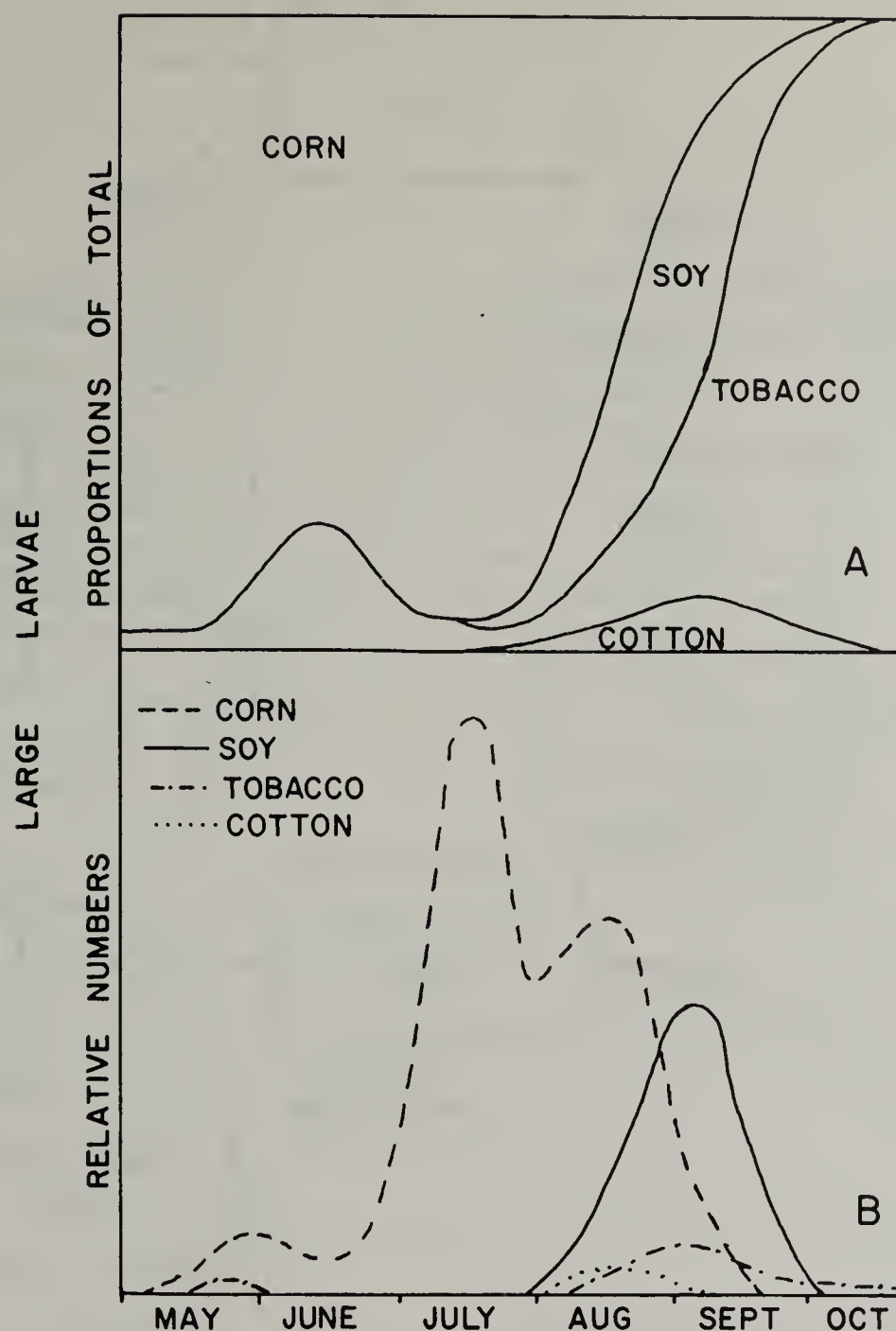


Fig. 1. —Generalized large larval production flow of *Heliothis zea* among the 4 major hosts in North Carolina: (A) relative total numbers, (B) relative proportions.

to stage. A major factor setting upper limits is food. “Food”, within the context of this species’ inherent characteristics, refers to the number, type and quality of feeding sites available per hectare, as well as the total hectares of host plants. Thus, the biomass (acreage) of the principal hosts must be included. The effect of weather and natural enemies on the life processes and mortality at each step must also be represented.

The data and first mathematical representations of relationships and processes were very rough approximations, many of which we still retain. We have attempted to improve many of these approximations by detailed modeling and research on each step in the flow. Figure 3 depicts the elements in the more detailed flows from stage to stage.

In this presentation, we would first like to briefly discuss our total data base and then the model components which have been derived from these data.

Data Source

A vast source of data is available on the physiology, behavior, host relationships and mortality factors of *H. zea* and much of this information has been incorporated in our modeling effort. More data will have to be used as the model is refined, and these refinements will depend largely on the cooperation of physiologists, behaviorists and other specialists in modifying model components. Due to the large number of references dealing with *Heliothis*, it was necessary to develop a reference file and computerized search capabilities. We presently maintain a reprint collection and keyword searchable file, using INFO360 (Rich et al. 1973) which contains over 3000 entries. This bibliographic research has been in cooperation with Dr. Douglas K. Sell, Illinois Natural History Survey, who is preparing a comprehensive *Heliothis* bibliography for publication. Earlier reviews of

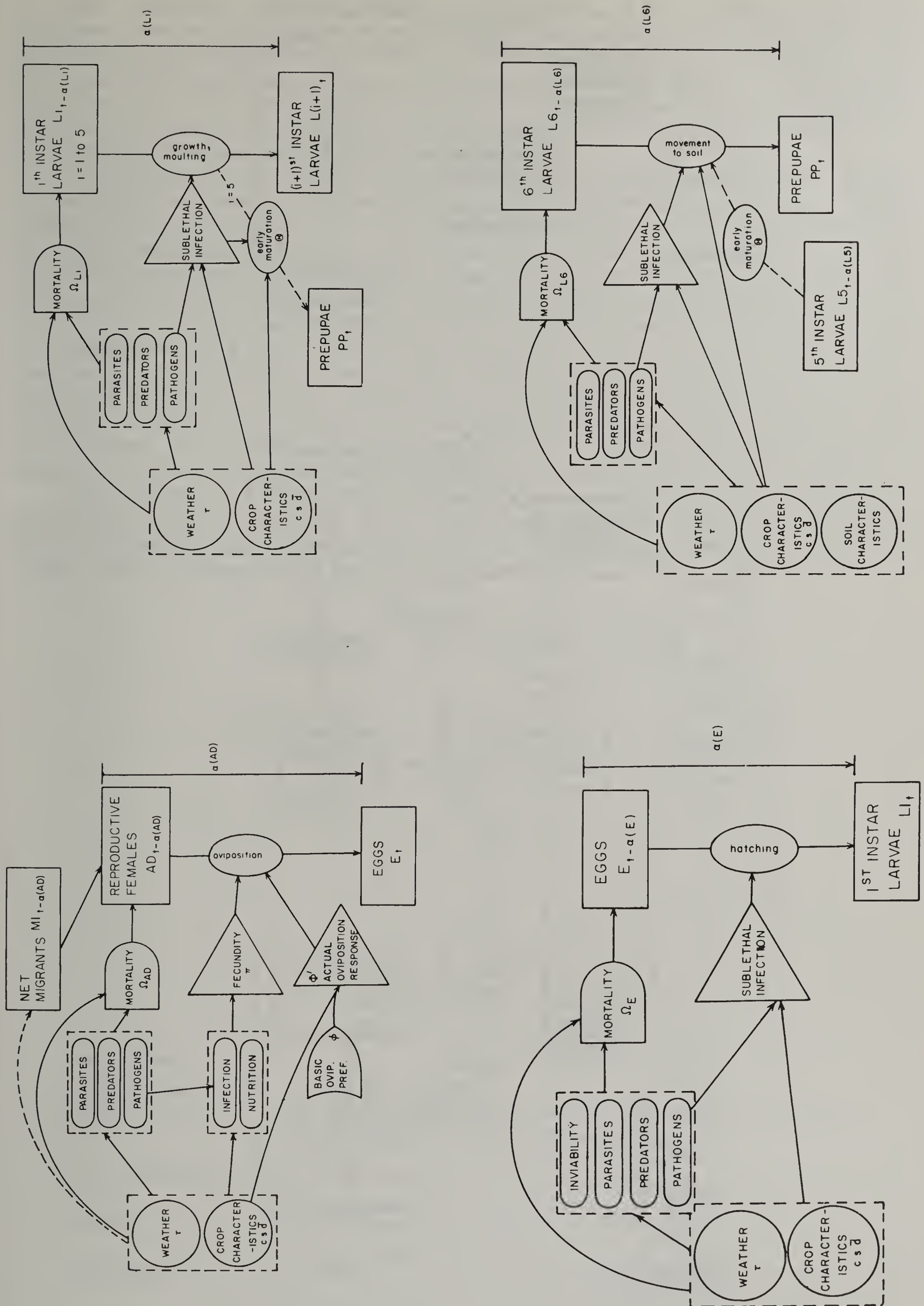


Fig. 3. –Detailed stage to stage flows, illustrating the major components of the *H. zea* life system.

Basic assumptions relative to reproductive potential were a 1:1 sex ratio, a temperature-dependent preoviposition period, and a fecundity and temporal ovipositional pattern also temperature-dependent (Isely 1935). Ovipositional preference data from our research (Johnson et al. 1975) were used in partitioning the eggs among the host crops. Data on incubation and larval periods reported by Isely (1935) were expanded and validated for local strains and conditions. Although data presented by Fye and McAda (1972) for a laboratory strain of *H. zea* are more detailed, they were found to be inapplicable to the wild North Carolina population.

Larval populations were monitored weekly from the time of spring emergence (early May) until the first killing frost (October-mid November) from 1970 through 1975, in from 1-3 large study areas in North Carolina. In each study area, counts were made on a minimum of 6 (usually 10) fields of each of the 4 major host plants (corn, cotton, tobacco and soybeans). Larval sampling in tobacco and cotton was accomplished on a basis of visual counts of larvae on a per plant and per row-foot basis. The beat cloth method of sampling (Deitz et al. 1976) was used in soybeans. Sampling in corn was found to be more efficient on a feeding site rather than a plant or row-foot basis. Regardless of the crop, samples taken on a plant or row-foot basis incorporate 2 sources of variation: (1) the variation associated with the distribution of larvae among feeding sites, and (2) the variation in the number of feeding sites per plant or row-foot. This latter source of sampling error is particularly great in corn. By using a feeding site (i.e., corn ear) as the basic sample unit, the sample variance is greatly reduced (in the example shown in Fig. 4, from 2.07- 0.68 times the mean). With independent estimates of feeding sites/hectare, larval populations were estimated more accurately and with fewer samples.

Upon completion of feeding, full-grown larvae leave the plant, burrow into the soil, form a pupal cell and pupate. These pupae either continue development into the adult stage or remain as quiescent, diapausing pupae for overwintering. There are 4-5 generations of *H. zea* per year in North Carolina, with the later generations overlapping extensively.

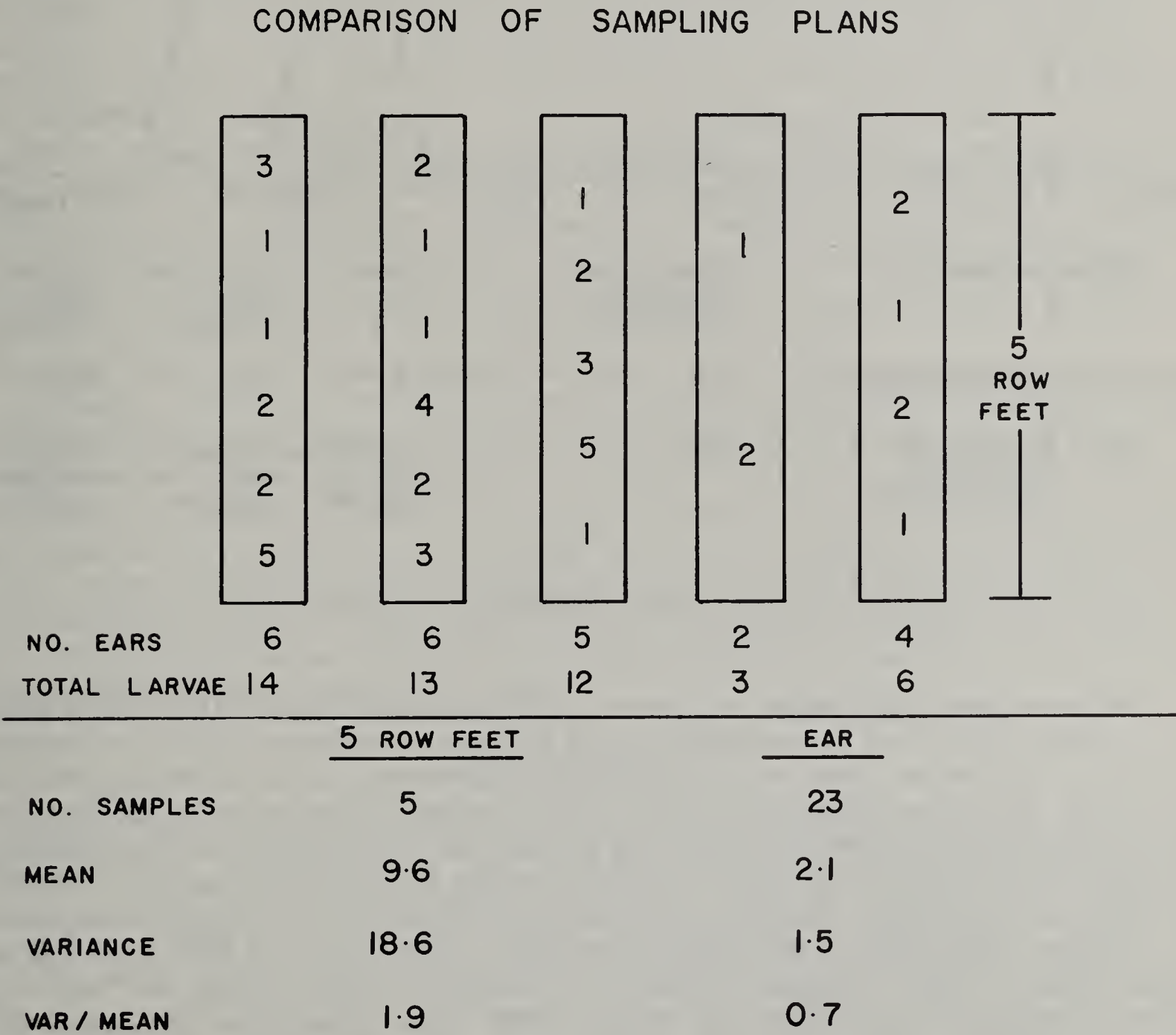


Fig. 4. –Comparison of per feeding site versus row-foot sampling.

Figure 5 is a generalized curve depicting relative adult density based on our records from light traps operated from April to November each year. At the bottom of the graph, the principal source of each moth flight as well as the principal hosts on which each flight oviposits is indicated. Late season moth flights, however, are strongly influenced by the advent of pupal dormancy, which is initiated through the combined effects of photoperiod, temperature, and nutrition during, at least, the egg and larval periods (Phillips and Newsom 1966, Mangat and Apple 1966, Wellso and Adkisson 1966, Roach and Adkisson 1970). The incidence of this pupal diapause rises from a low level in late July to almost 100% by late September, as determined by rearing field-collected, last-instar larvae over a 4-year period.

The second large category of data required is information on environmental factors. Weather is the dominant, essentially non-reactive factor influencing all components of the life system. The direct effects of its variable elements (temperature, moisture, etc.) on *H. zea* alter not only behavior but also rates of development, fecundity, and survival. Its effects on host plants, natural enemies and cultural practices also regulate their synchrony with, and impact on, *H. zea*.

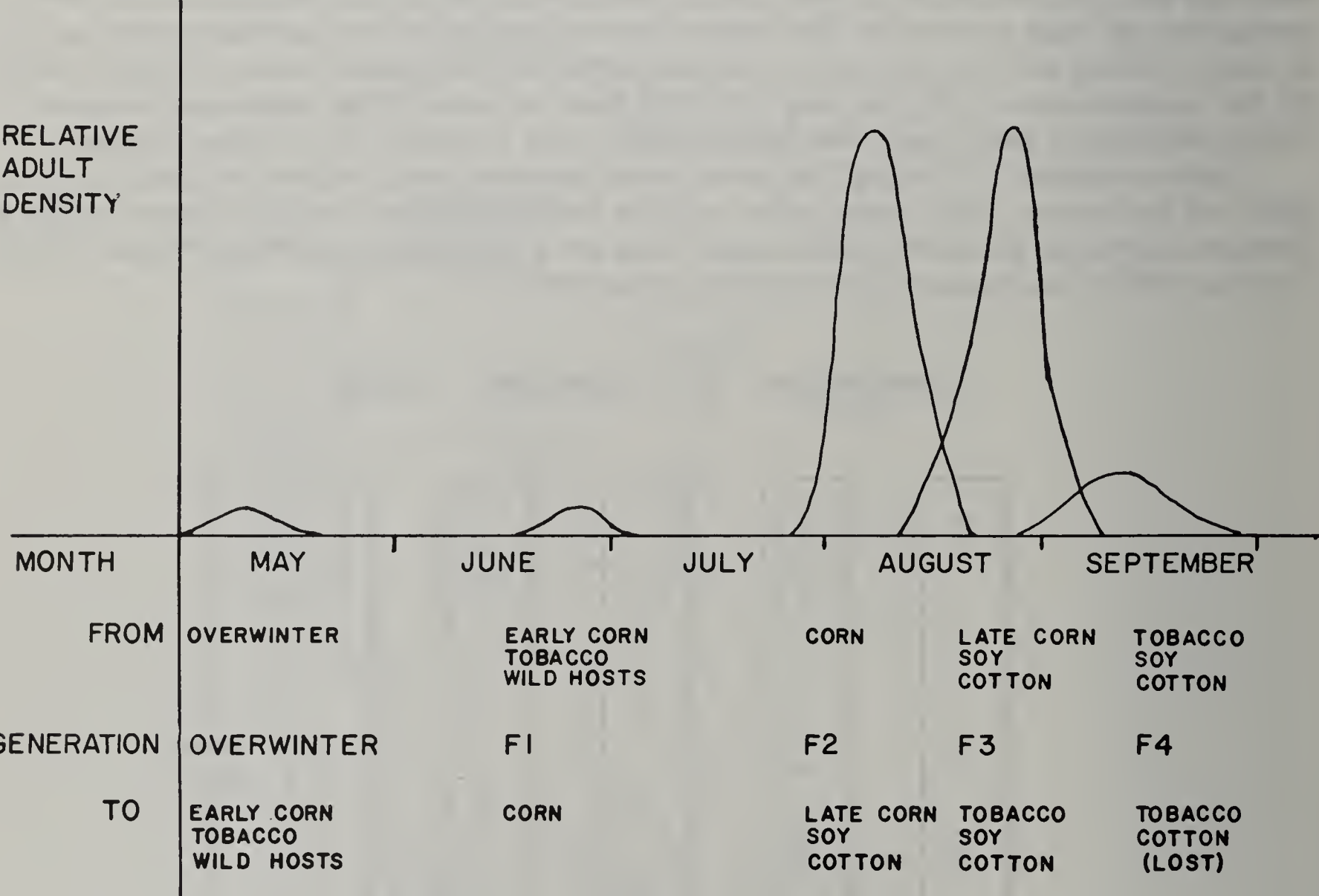


Fig. 5. —Generalized pattern of adult *H. zea* in North Carolina.

The kinds (host plant species and phenological states) and quantity (biomass or acreage) of food vary from area to area and seasonally. A key host in early season may be of no significance in late season, and vice-versa. Thus seasonal production is dependent upon a complex of hosts through which the *H. zea* biomass flows from spring to fall. Population components on different hosts also differ in rates of development, fecundity and survival due to nutritional and microenvironmental differences, and mortality of *H. zea* from natural enemies is influenced by factors intrinsic to host plants (see next paragraph). Emphasis in our study was placed on the population components on corn, soybeans, tobacco, and cotton, which collectively occupy about 1 ½ million hectares in North Carolina. Data on gross acreages of each were obtained for annual issues of “North Carolina Agricultural Statistics” (e.g., Kibler and Hinson 1975). These acreages were partitioned each year according to phenological states through weekly surveys in selected study areas. Spatial arrangements were determined through the use of aerial maps and ground surveys.

Crop management practices strongly influence spatial and temporal patterns and equilibrium levels of *H. zea*, and act largely as non-reactive factors, except when used facultatively for temporary suppression of population foci on the basis of the economic threshold principle. Independent farmer decisions collectively determine the kinds, quantities and spatial arrangements of the major host plants. In addition, they influence the seasonal availability, attractiveness, and suitability of hosts for *H. zea* through varietal selection, planting date, fertilization and other cultural practices. The nature and timing of these practices can cause significant direct mortality on *H. zea* (for example: tillage which destroys many potentially overwintering pupae) and may influence the impact of natural enemies.

The natural enemy complex is responsible for a large portion of the *H. zea* mortality and varies widely from generation to generation, place to place and from one food plant species to another. The wide host range of *H. zea* seems to be matched or exceeded by most of its natural enemies, none of which are known to be strictly host specific. Since adults of each *H. zea* generation tend to disperse widely to new hosts, each generation becomes at least partially disengaged from those natural enemies generated by the previous generation. This tends to dampen density associated numerical responses as well as limiting the potential of functional responses of localized natural enemy populations.

The effects of each natural enemy species differ markedly according to the host plant species and its phenological state. For example: *Trichogramma* spp., egg parasites, at times inflict heavy mortality in corn (see general reviews of *H. zea* cited above for many specific references) but not in tobacco (Nuenzig 1969) due to the inhibitory, physical and chemical properties of the tobacco foliage (Rabb and Bradley 1968). By the same token, larval and pupal parasites (principally tachinids, ichneumonids and braconids) commonly take a heavy toll of *H. zea* on tobacco (Irabagon 1973, Hughes 1975), soybeans and cotton (when not disrupted by insecticidal treatments) but have little effect on larvae feeding within the protective husks of corn ears (Nuenzig 1969, Hughes and Rabb 1976).

Gross environmental heterogeneity (i.e., kinds and acreages of crops and uncultivated areas) may be related to differences between agroecosystems in natural enemy complexes on specific crops. For example, Deitz et al. (1976) found striking differences between coastal and central North Carolina agroecosystems in the predator complex in soybeans. Some enemies characteristically have little or no impact on some generations of *H. zea* but significant effects on others. For example: Danks (1975a) found *Winthemia rufopicta* (Big.) parasitizing *Heliothis* spp. on tobacco in North Carolina only during late summer and fall, when *Heliothis* mortality from this and other tachinids increased markedly. His (Danks 1975b) comprehensive and penetrating study of factors determining levels of parasitism by *W. rufopicta* illustrates clearly the necessity of measuring a very large number of factors if the ecology of this parasite is to be synthesized in a manner useful in modeling. This conclusion is true in large measure for each of the many *H. zea* enemies.

Mortality inflicted by disease organisms also varies widely, spatially and temporally. Due to the high reproductive potential of the microorganisms involved, diseases can and often do suppress localized infestations more rapidly and usually more completely than other natural factors. Such epizootics, however, are strongly dependent on threshold levels of inoculum (often produced in alternate hosts) and favorable weather conditions. In North Carolina, a polyhedrosis virus and a fungus, *Nomuraea rileyi* (Farlow), are frequently associated with *Heliothis* populations (Neunzig 1969). The fungus often inflicts heavy mortality on *H. zea* in soybeans (Sprenkel and Brooks 1975). Other microorganisms such as *Nosema heliothidis* Lutz and Splendore (Brooks 1968, Gaugler and Brooks 1975) and *Chromonema heliothidis* Khan, Brooks and Hirschmann (Khan et al. 1976), may alter developmental rates and influence mortality.

Model Components

HELSIM-2 is a computer simulation model, written in FORTRAN IV, which allows for the simultaneous tracking of populations in up to 14 different field types (i.e., specific combinations of crop and crop growth sequences). It requires approximately 365K and 6 minutes on an IBM 370/65 for a complete run. The parameters whose values are set within the program are listed in Table 2, the input required is presented in Table 3, and the output provided is given in Table 4. For the purpose of examining our present model, each component is presented separately, but because of the various interactions among components, results of simulations using each of these submodels must be presented in the context of the total model.

Table 2.—Constants set within the HELSIM-2 program.

- A. Temperature-dependent functions
 - 1. Developmental rate and distribution constants
 - 2. Fecundity constants
- B. Host and time related functions
 - 1. Basic ovipositional preference vector
 - 2. Daily miscellaneous mortality rate constants
 - 3. Cannibalism function constants.

Table 3.—Acronyms and definitions of input variables for HELSIM-2.

Variable Name	Definition
TITLE	Title for simulation.
ND1	First emergence of overwintered adults (Julian date).
ND2	Last emergence of overwintered adults (Julian date).
NDEND	Last date for simulation (Julian date).
NK	Number of field types (14 maximum).
NC	Number of crops (14 maximum).
TFA	Total hectares of farmland in county.
FLABEL	Descriptive titles for each field type.
ADULT	Running 2-day averages of emerging adults from ND1 to ND2.
EAR	Average number of primary feeding sites per .001 hectare, by week and field type.
BCAN	Number of secondary feeding sites per primary site, by week and field type.
KROP	Crop index for each field type.
CEI	Canopy index by field type.
AC	Hectares of each crop in county.
ISTATE	Index for actual maturity state of each field type by week.
PCT	Proportion of the respective crop represented by each field type.
TMAX	Daily maximum temps for year.
TMIN	Daily minimum temps for year.

Table 4.—Output produced by HELSIM-2.

- 1. Input variable values.
- 2. Actual ovipositional response probability function.
- 3. Number of individuals entering, and in, each stage, by date and field type.
- 4. Total number of moths in county, by week.

During the growing season, the temporal and spatial patterns of production potential of *H. zea* larvae and pupae are determined by the adult ovipositional responses (i.e., eggs laid per hectare on each specific host). These responses are determined, in a stochastic sense, by three sets of variables: (1) the basic ovipositional preferences, ϕ , of *H. zea* for specific crops and crop maturity states (i.e., the relative attractiveness of equal-sized fields of all hosts located equidistant from a population of moths), (2) the spatial and temporal patterns of these hosts, and (3) the spatial and temporal coincidence of ovipositing females with host plants in each of their phenological stages available.

Johnson et al. (1975) have shown that the actual ovipositional response probability function, G_{jit} , (proportion of eggs oviposited on a specific crop j in a specific maturity state i at time t , given the observed agricultural crop matrix) is given by

$$G_{jit} = \left[(\phi_{ji}) / (D^2_{jit}) \right] / \left[\sum_k \sum_l (\phi_{kl}) / (D^2_{klt}) \right] \quad (1)$$

D_{jit} is the average distance from a moth of fields of crop j in state i at time t . At present, D_{jit} is calculated from the proportion of each crop in a particular maturity state, using a modification of the nearest neighbor index (Clark and Evans 1954).

The actual ovipositional response (eggs/hectare), E_{jit} , is then given

$$E_{jit} = \frac{(A_t) (SR) (FEC_t) (G_{jit})}{Hec_{jit}} \quad (2)$$

where

A_t = total adults at time t

SR = sex ratio (♀/total)

FEC_t = fecundity (total eggs laid on day t /♀)

Hec_{jit} = hectares of crop j in state i at time t

Estimates of the ϕ values were obtained from greenhouse and field cage experiments and the submodel validated with field survey data from several coastal plain counties of North Carolina. The following assumptions concerning the intrinsic characteristics of *H. zea* were used in developing this submodel:

- (1) There exists a basic ovipositional preference vector, whose elements, ϕ , describe quantitatively the relative attractiveness of specific hosts in specific phenological states.
- (2) The proportion of eggs laid on a specific host is proportional to the average stimulus received from that host divided by the sum of the stimuli from all other hosts (Eq. 1).

With respect to environmental heterogeneity, this submodel is valid only when host fields are small and nearly equal in size, and are randomly distributed with respect to each other and with respect to the sources of ovipositing moths. This assumption has been tested and found valid for several areas in the North Carolina coastal plain. In regions such as Texas or California, where large and variable acreages of a single host crop are found, the submodel would have to be altered to varying degrees. If only nonrandomness were involved, merely a correction in the calculation of the D_{jit} values (see Eq. 1) would be necessary. However, in areas with large differences in field size, factors such as rate of movement and longevity of adults, as well as "masking" effects of large fields might have to be represented in the model.

In contrast, since MOTHZV-2 (Hartstack et al. 1976) utilizes empirically determined rates of migration from corn, sorghum, and cotton (also based on crop phenologies) it is specific for the Texas agricultural system. Thus field size and distribution considerations present no problem in using

MOTHZV-2 as long as the empirical rates are accurate and the cropping patterns and cultural practices presently in use are retained.

The basic preference, ϕ , of moths to a particular host is a function of many factors such as host species, host maturity, vegetative canopy development, water stress, plant pathogens, etc. At present we have partitioned these preferences only by host species, maturity, and canopy, the two former under experimental conditions. Since small plot and cage experimentation has not proven suitable for determining the exact effects of canopy, we have had to use relative counts of small larvae in adjacent fields with varying canopies as rough estimators of the differential response of moths to varying degrees of canopy development.

Development

Once the spatial and temporal pattern potentials (in terms of eggs laid) have been set, numerous factors having both direct and indirect effects on survival then determine the actual realization of this potential in terms of larval and pupal production. Temperature is one such factor whose importance appears to be as much indirect as direct in that it is an important driving force in the species dynamics. It has been necessary to describe development as a stochastic process and 2 algorithms are used for this purpose. The first algorithm mimics the developmental rate, R_τ , of a single individual (e.g., the fastest or slowest individual) as a non-linear function of temperature, τ , (Stinner et al. 1974):

$$R = C / (1 + \exp(k_1 + k_2 \tau^1)) \quad (3)$$

where $\tau^1 = \tau$ for $\tau \leq \text{topt}$

$$\tau^1 = 2 \cdot \text{topt} - \tau, \text{ for } \tau > \text{topt}$$

C, k_1, k_2 = empirical constants

topt = optimum temperature

The second algorithm (Stinner et al. 1975) uses the first, with separate parameter estimates for individuals exhibiting the fastest, slowest, and median developmental rates. It calculates a cumulative probability of completion of development and, thus, describes the variability observed for a given temperature regime. Given estimates of the developmental times for the fastest (A), slowest (B), and median (M) individuals under any temperature conditions, the probability, $P(t)$, that an individual will have developed to the next stage by time t is given by:

$$P(t) = (1-z)^{\theta z^2} \quad 0 \leq z \leq 1 \quad (4)$$

where $z = (B-t) / (B-A)$

$$\theta = \ln(.5) / \left[x^e \ln(1-x) \right]$$

$$x = (b-M) / (B-A)$$

MOTHZV-2 utilizes a normal distribution for development in a manner similar to that described for HELSIM-1 (Stinner et al. 1974a). Although the time requirements for simulating this variability are somewhat less using a normal distribution algorithm than with the algorithm above, we found wide discrepancies between observed distributions and the normal distribution at extreme temperatures. However, to our knowledge, sensitivity analyses have not been conducted to determine the effect of these errors on the overall behavior of either model. The inclusion of this variability, however, is necessary to accurately depict the discrete to overlapping generations which occur as the season progresses and which determine the synchronization of adult flights with various hosts. Added importance of this variability will be discussed shortly.

In setting the temporal pattern potential, the effects of nutrition cannot be overlooked. Several authors have demonstrated these effects (Isely 1935, Phillips and Barber 1929), but at present the

quantitative data necessary to incorporate these effects are not available. Research is presently being conducted by Dr. George Shaw (pers. com.) to provide these data, utilizing diets which mimic the changing nutritional status of host plants as they mature. His results will be incorporated into HELSIM-2.

Cannibalism

Given both the spatial and temporal pattern potentials, we can begin to examine the actual mortality factors. These factors and their levels vary both spatially and temporally, with certain specific patterns being associated with specific host crops, cropping patterns and cultural practices.

Perhaps the most important of these mortalities, at least from the population regulation viewpoint, is cannibalism or "intraspecific predation." With *H. zea* and its prime host, corn ears, we have an example of intraspecific competition without food resource limitation. This at first appears to be a serious waste of energy since mortalities in excess of 75% are not unusual and the larvae apparently gain no added nutritional benefit from feeding on other larvae (Barber 1936). It is therefore necessary to hypothesize on the evolutionary origin of this process to gain insight into this apparent "mistake". If one looks for the probable original host of *H. zea*, one finds the precursors of corn-small plants with 1-3 small ears (2-3") located immediately below the tassel. It can be concluded that these ears could support to maturity only a single larva each. The evolution of cannibalism under these conditions seems understandable.

The submodel developed for cannibalism (Stinner et al. in press) calculates the spatial distribution of larvae (and, thus, the probability of contacts between larvae). From these probabilities and the probability of death given a contact, the mortality is calculated.

$$\Psi_i = 1 - \left\{ \left(\sum_{k_i=1}^{m_i} (\beta_{ii})^{k_i-1} P(R_i) R_i \right) \left(\prod_{j=i+1}^6 \left\{ \sum_{k_j=0}^{m_i} (\beta_{ij})^{k_j} P(R_j) \right\} \right) / \bar{\chi}_j(t) \right\} \quad (5)$$

where

Ψ_i = mortality on i^{th} stage larvae during time interval Δt ($=0.1$ day)

β_{ij} = probability that an i^{th} stage individual is not killed by a j^{th} stage individual during Δt , given both individuals at the same feeding site.

$P(k_i)$ = probability of having $k_i - i^{\text{th}}$ stage larvae at a single feeding site ($0 \leq k_i \leq m_i$).

$\bar{\chi}_i(t)$ = mean number of i^{th} stage larvae per feeding site at time t

m_i = maximum number of i^{th} stage larvae per feeding site.

Cannibalism acts to alter both survival and temporal patterns, and is, conversely, affected by developmental variability and, to a lesser extent, spatial distributions of larvae. In order to more fully understand the effects of cannibalism and the relative importance of the various components (e.g., spatial and temporal distributions, larval density), numerous sensitivity analyses were conducted on this submodel. These analyses involve simulations in which we hold all but one set of parameters constant and then observe the behavior of the model as we vary that one parameter set.

The submodel is not very sensitive to manipulations of the distribution of larvae among feeding sites (Fig. 6), until a high degree of contagion is reached (in this case, as measured by the negative binomial k parameter). The slight effect of clumping on mortality ($100 [1-F_2 \text{ Adults}/F_1 \text{ Eggs}]$) becomes less noticeable as initial adult density increases.

The effect of cannibalism on timing of moth peaks (apparent generation peaks) is striking (Fig. 7). Since cannibalism serves to eliminate a larger proportion of larvae from the last than the first eggs laid (and the slower developing individuals), the time from peak to peak of adult moths decreases as egg and larval density increases. This is more pronounced in ecosystems where a large proportion of the *H. zea* population is on a host plant, such as corn, where the number and structure of feeding sites is restrictive and cannibalism, therefore, is intense. In simulations where initial adult densities were comparable to those observed in natural populations, the time from one peak of moths to another

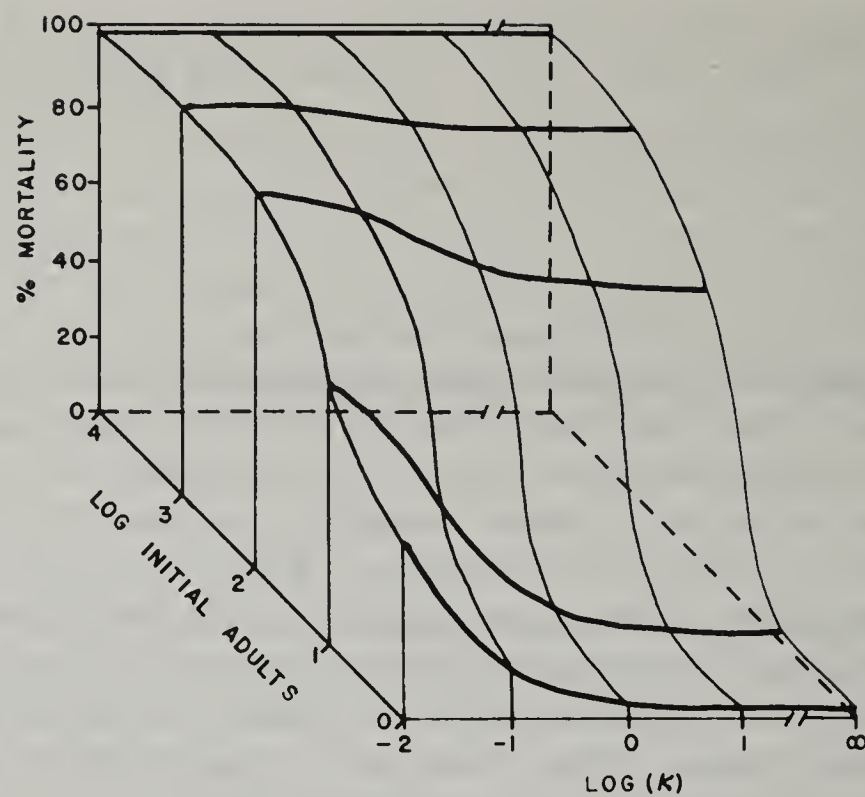


Fig. 6. —Effect of spatial distribution of larvae (as measured by the negative binomial k parameter) on mortality caused by cannibalism.

was as much as 18% less than the time that would have been predicted on the basis of temperature-dependent developmental rates alone. For example: where generation time was predicted to be 30 days on the basis of temperature-development data, the actual time from one moth peak to the next was only 25 days. In addition, at high initial densities, a secondary “wave” is also produced. Thus temperature alone cannot be used to predict the timing of moth flights or their synchrony with the various hosts, where a large component of the *H. zea* population occurs on a host plant conducive to intense cannibalism.

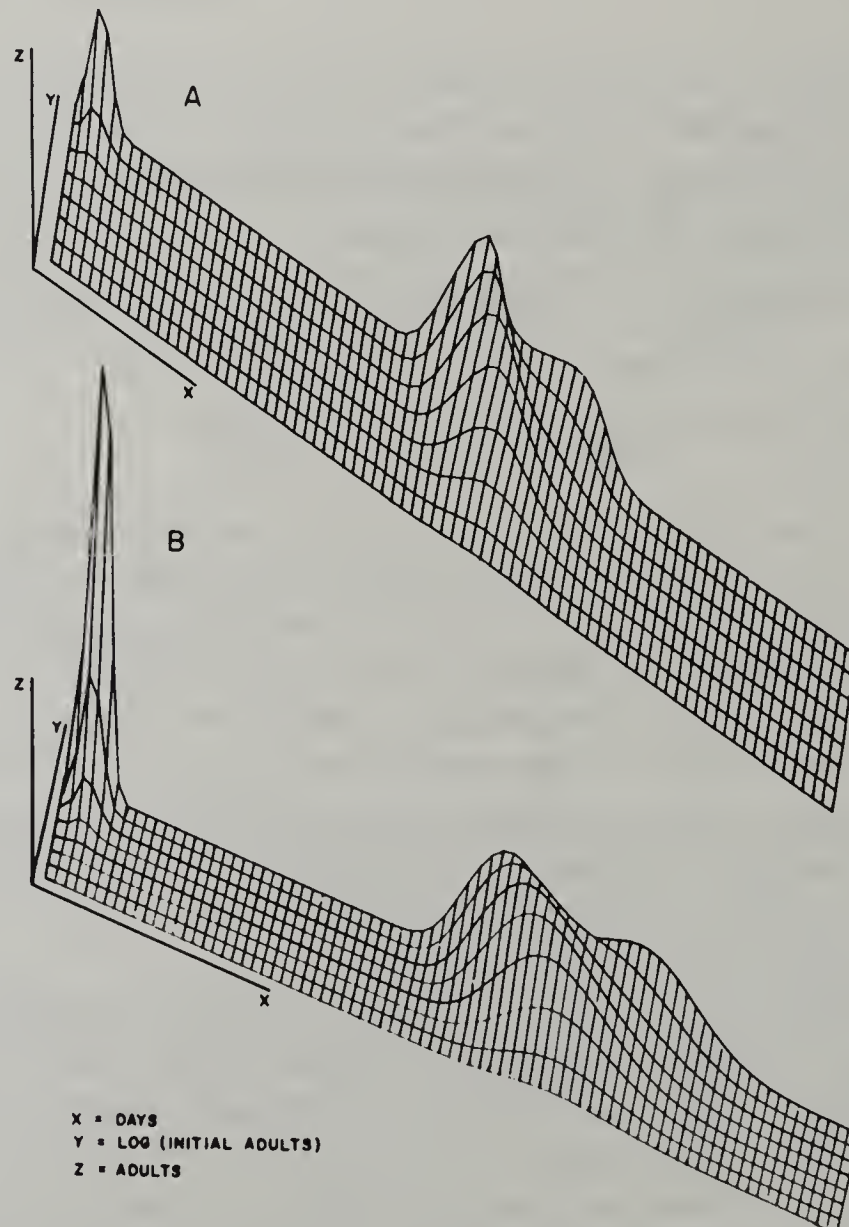


Fig. 7. —Adult populations over time for different initial adult densities: (A) utilizing actual developmental variability and (B) using case IV developmental variability (see Table 4).

It should be noted that this submodel is highly sensitive to the amount of developmental variability (Table 5). This sensitivity mandates the accurate inclusion of developmental variability in this or any other model of a species' dynamics in which contest-type intraspecific competition plays a significant role.

Table 5.—Effect of initial adult density and variation in larval development on apparent generation time. (Actual generation times for cases I through IV without competition were: 47, 48, 49, 50 days, respectively).

Initial Adult Density	Days (%) Reduction in Apparent Generation Time for Cases			
	I 13*	II 5*	III 7*	IV 9*
1	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
10	1 (2.1)	1 (2.1)	1 (2.0)	2 (4.0)
50	2 (4.3)	3 (4.2)	3 (6.1)	3 (6.0)
100	2 (4.3)	3 (4.2)	4 (8.2)	4 (8.0)
500	4 (8.5)	5 (10.4)	6 (12.2)	6 (12.0)
1000	4 (8.5)	6 (12.5)	6 (12.2)	7 (14.0)
2000	5 (10.6)	6 (12.5)	7 (14.3)	8 (16.0)
5000	5 (10.6)	7 (14.6)	8 (16.3)	9 (18.0)

*Time (days) between development of first and last individual (See Stinner et al. in press).

The basic assumptions of the cannibalism submodel are as follows:

1. The probability of death, given a contact between two larvae is a function of the respective age classes of the larvae. At present these probabilities are roughly approximated only for corn ears at 22°C.
2. The spatial distributions among sites for each age class of larvae are independent of each other and can be described by a negative binomial, or its limit, the Poisson.

In light of the submodel's insensitivity to spatial distribution, violations of this assumption would appear to have little effect on the overall model behavior. Additionally, sampling of actual larval distributions has shown them to not differ significantly from the Poisson. It should be noted that, in actual practice, some corn varieties with similar yields differ markedly in the type and number of ears produced. The production of secondary, non-grain producing ears (either singly on the stalk or at the same leaf axil as a grain ear) is highly variable, and several preliminary studies by the authors indicate that these secondary ears are not equivalent to grain ears in either the timing of their attractiveness to ovipositing moths or the number of *Heliothis* produced. The extent that they differ, however, has not been quantified accurately enough for use in HELSIM-2.

The refinement of the cannibalism submodel will require further research on the effects of temperature and other feeding site types (e.g., corn whorls, soybean pods, cotton squares, etc.) on mortality and survival rates. In North Carolina, where the major portion of *H. zea* biomass flows through corn, it is not possible to predict accurately the timing of moth flights on the basis of temperature-development relations alone, since cannibalism on corn shortens the observed peak to peak times. In areas where the major *H. zea* biomass flows through crops such as cotton and soybeans which have many more feeding sites (and thus much less cannibalism), prediction of flights based on temperature alone might prove more accurate than in North Carolina. Cannibalism is incorporated in MOTHZV-2, but in a form which reflects the effects of "large" larvae only.

At present, HELSIM-2 merely lumps predation, parasitism, disease and mortalities from undetermined causes into a daily miscellaneous mortality which is described as a function of crop, crop maturity, and time. For development of a more accurate general population model of *H. zea*, submodels for each of the major natural enemy species (or complexes) must be included. The large number and diversity of natural enemies, which vary from host plant to host plant of *H. zea*, make it imperative to establish research priorities in developing natural enemy submodels for the *H. zea* model. Since host plant complexes, along with their associated natural enemy fauna, vary widely among the agroecosystems within the geographical range of *H. zea*, priorities may be expected to be different from place to place. In each agroecosystem, however, it would be logical to give first priority to modeling the most important natural enemies or natural enemy complexes associated with the host plants generating the highest *H. zea* production potential. Obviously, criteria for importance must be established and will vary according to the objective for constructing the model.

The natural enemies which change the age specific mortality pattern may be very important in preventing damage from a given larval infestation but have little effect on generation survival. On the other hand, an enemy responding directly to the density of mature larvae (after most of the generation mortality has been inflicted) may have little effect in preventing damage from a given infestation but may have a pronounced effect on the population level of the next generation. Predators present a particularly intractable problem because so many species are involved, they are so polyphagous, and their individual effects on *H. zea* are so interdependent with the actions of the total predator and prey complex. Practical considerations make it probable that the more effective inclusion of predation in *H. zea* models will be through the use of more accurate submodels reflecting the pooled effects of a predator complex as associated with each major *H. zea* component as defined by food plant type.

MOTHZV-2 includes the effects of both general predation (as an empirical function of time and crop phenology, similar to the miscellaneous mortality component of HELSIM-2) and parasitism. The parasitism submodel utilizes either empirical rates or a modification of Nicholson and Bailey's (1935) "area of discovery" as proposed by Knipling and McGuire (1968). Theoretical studies of parasitism have raised considerable doubts concerning the applicability of Nicholson and Bailey's "area of discovery" to wild populations, and alternative approaches have been suggested (Stinner and Lucas 1976). The utility of these approaches for analyzing a system as complex as that exhibited by *Heliothis*, involving multiple crops and multiple parasites (which have alternate hosts), however, has yet to be demonstrated.

The problems involved in modeling insect diseases are similar to those previously mentioned with respect to parasites and predators. However, disease organisms tend to be more sensitive to both weather and the availability of alternate insect hosts at high densities. This sensitivity, coupled with the rapid exponential growth capabilities of pathogens and our inability to predict weather, make accurate projection of disease incidence most difficult, even with highly refined models.

Diapause

The within season production of adults from larvae and pupae decreases proportionally after mid-season as an increasing proportion of larvae develop into diapausing pupae. Although considerable information is available on the effects of photoperiod and temperature (as experienced by parental adults, eggs, and larvae) on the induction of pupal diapause, we have been unable to find a mathematical expression describing the observed diapause incidence curve which fits the empirical data better than a simple sigmoid time function (Fig. 8). This function thus, is used to partition prepupae into developing and diapausing pupae. At present, the model cycles developing pupae back into the population as reproductive adults, but merely "stockpiles" the diapausing pupae. The eventual fate of these diapausing pupae is the subject of much of our present investigative efforts.

Simulations

Although the present model has many imperfections, we would like to briefly, and with many reservations, present results of a few of our simulations. Table 6 lists the actual and simulated large

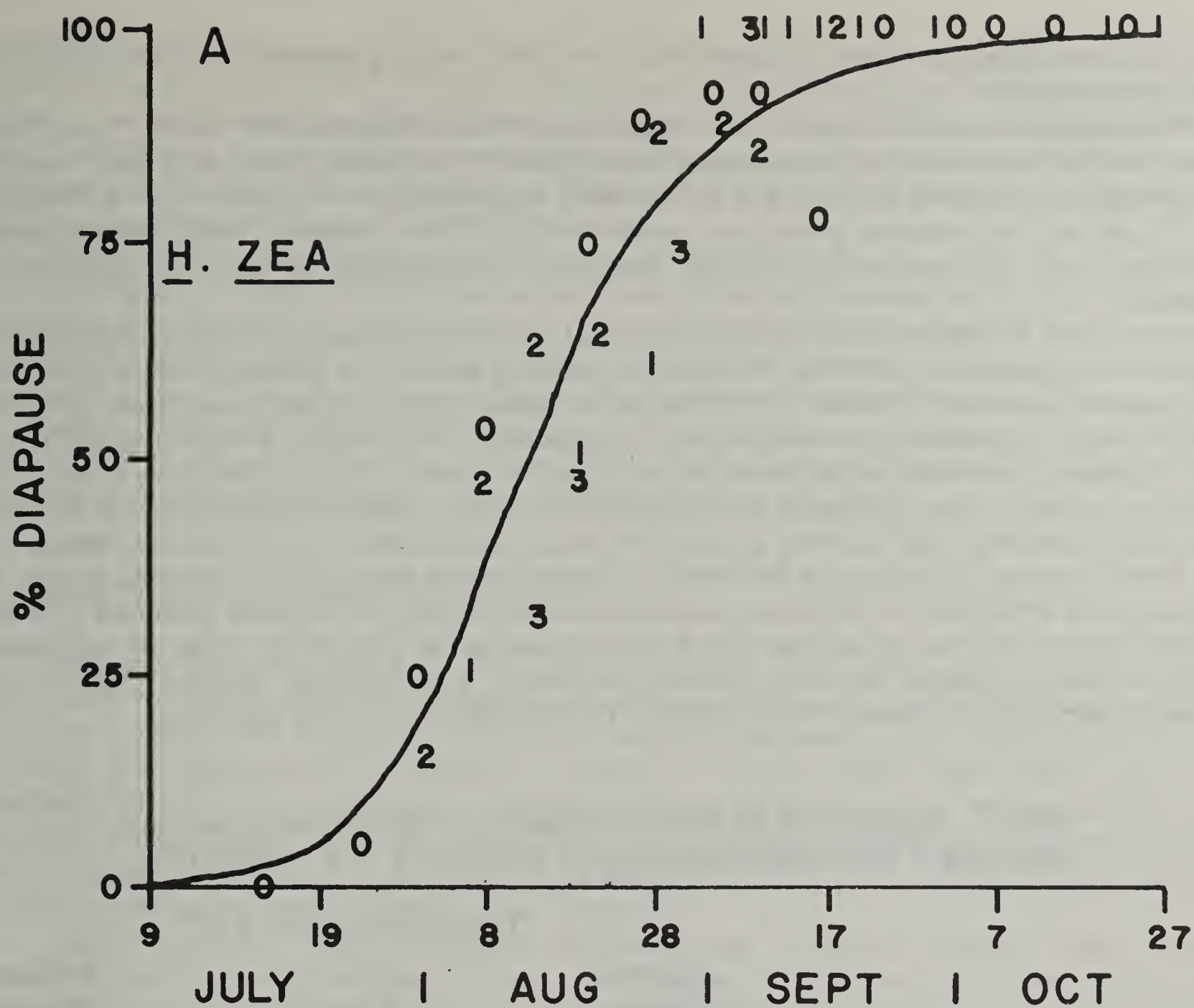


Fig. 8. —Diapause incidence curve for *H. zea* in North Carolina. The numbers 0-3 reflect actual data for the years 1970-1973 respectively.

Table 6.—Julian dates for simulated and observed *H. zea* large larval peaks in Johnston Co., N.C., during 1970.

Field type ¹	Observed Peaks	Simulated Peaks
Corn 177	162, 196	163, 199
Corn 184	167, 204, 231	164, 202, 230
Corn 191 +	167, 210, 231	164, 202, 240
Open Soy	244	241
Inter Soy	237	240
Closed Soy	237	240
Tobacco	244, 281	240, 283
Cotton	244	248

¹ See text for explanation of codes.

larval peaks in Johnston County, North Carolina, for the cropping system and cultural practices observed during 1970.

The numbers after corn refer to the Julian date of first silking and the “open”, “inter” and “closed” before soybean refer to the canopy development. Since larval counts were made weekly, the observed peaks may be in error by ± 6 days. With the exception of one peak for corn silking on day 191, all of the simulated peaks were within 4 days of the observed. Predictions of actual population levels, however, are still highly inaccurate, but generally by less than an order of magnitude.

One use of simulation is to examine the potential effects of changing cultural practices over a wide area on populations of *H. zea*. Simulations involving altering the planting dates of corn have been published previously (Stinner 1975). Here we examine the hypothetical cases where all of the soybean acreage is planted either early or late, as opposed to the present 6-8 week planting period (Table 7). When soybeans are all planted early, there are only minor changes in the *H. zea* populations in corn and tobacco, when compared to the standard. In cotton, a slight decrease (8.3%) in prepupal production is observed. This decrease is related to the increased acreage of soybeans blooming at the same time as cotton, resulting in an increased proportion of eggs being laid on soybeans. In spite of this increase in oviposition on soybeans, the uniform early planting of soybeans produced 25% less prepupae in soybeans than in the standard. When soybeans are all planted late, there are only minor changes in the populations on corn, tobacco and cotton. Late planting, however, yields a 22% increase in prepupae in soybeans over the standard (a 63% increase over early planting).

Table 7.—Simulation of the effects of changes in soybean planting date on season-long *H. zea* prepupal production in Johnston Co., N.C., during 1971.

Crop	Hectares	Standard Planting Variability	Prepupal Production x 10 ⁶	
			All Late Planted (% Change) ^a	All Early Planted (% Change) ^a
Corn	30,582	321.3	316.8 (-1.4)	325.7 (+1.4)
Soybean	13,735	159.3	193.8 (+21.7)	119.1 (-25.2)
Tobacco	6,727	17.5	17.4 (-0.8)	17.6 (+0.8)
Cotton	622	1.9	1.9 (+1.0)	1.8 (-8.3)

^a% change from standard.

When considering *Heliothis* alone, earlier planting would seem, then, to be of benefit. The dynamics of other pests such as the Mexican bean beetle, *Epilachna varivestis* Mulsant, however, are also involved and must be considered in any planting date optimization.

Current and Future Research

Inter-Year Dynamics

Research and modeling has been devoted largely to within-season population dynamics and has not been adequate to link year to year dynamics. While data have been obtained on the production of diapausing pupae (and this production modeled), knowledge of the mortality and survival of field

populations of diapausing pupae is too imprecise to develop a submodel useful for depicting interyear flows. Having determined the foci of pupal production through sampling and simulations, and having a fairly accurate assessment of the incidence of diapause (Rabb et al. 1975), the relative importance of each of the foci to successfully overwintering *H. zea* must be determined. One study essential to this determination is the characterization of diapause intensity in North Carolina populations of *H. zea*, as accomplished by Holtzer et al. (1976a and b).

Research in progress involves two phases being developed simultaneously. The first involves in-field studies of the effects of soil type on pupal survival and adult emergence, utilizing field to field comparisons and small (3 x 3m) plots of 3 major North Carolina soils (eroded Appling, Norfolk sandy-loam and Plymouth loamy-sand). The second phase involves laboratory studies of the interactive effects of soil type, temperature, and soil moisture on survival of diapausing pupae. The completion of these two phases should establish moth production potentials for the pupal foci under existing soil and weather conditions. Research must next clarify the influence of extrinsic biotic factors and soil management under existing conditions on these potentials.

Integrating HELSIM-2 With Other Pest Models

The population dynamics of *H. zea* also is affected by other herbivores on its host plants and particularly by control efforts taken against associated pests. Thus, for more refined models of *H. zea* as well as models of pest complexes, which can be useful in optimization of control efforts, the *H. zea* model must be integrated with models of other pests and other crops. A single field modification of the *Heliothis* model has already been integrated with an initial model for the tobacco hornworm, *Manduca sexta* (Reagan 1975) on tobacco and we are presently involved in integrating HELSIM-2 with a Mexican bean beetle, *Epilachna varivestis* Mulsant, model as well as laying the groundwork for adding a model of the bean leaf beetle to the complex.

The inadequacies of our knowledge are easily seen — in basic research, model building, validation, and application to pest problems. Modeling at the wide-area population level, however, provides a comprehensive view of factors and processes influencing at least the major components of the *H. zea* system and provides an improved basis for assigning priorities in research. Some obvious areas for more intensive research are: (1) population components on additional host plants (including wild hosts); (2) natural enemy action; (3) long distance moth displacement; (4) modifications of the submodel dealing with inter-crop movements to make the assumptions relative to field size and field dispersion less restrictive; and (5) direct and indirect effects of various pesticidal use patterns. In addition, every component in the present model is but a rough approximation of the real world. Thus, this model is not an end, it is only a beginning, and presents a challenge not only to modelers, per se, but to physiologists, behaviorists, and other scientists, whose research is at lower organizational levels, to suggest modifications to various model components which would allow it to more realistically and accurately reflect population variations.

Summary and Discussion

Our modeling effort has provided a framework for the organization and use of data in achieving a more complete understanding of *H. zea* population patterns. In fitting data from a realistic deme (over a wide area in North Carolina) into this framework, we have been able to apply some existing knowledge more fully and focus attention on research needs.

We feel that the wide-area approach represented by our project is not only of potential but is essential to the continuing development and validation of ecological theory. At the First International Congress of Ecology, Whittaker (1975) drew attention to “a striking, and unwelcome, feature of ecology which has been the lack of a bridge of logical development and common understanding between population ecology and community ecology”. The contributions of Wellington and his associates (Wellington et al. 1975) to an understanding of the dynamics of wide-area populations of *Malacosoma californicum pluviale* (Dyar) is an outstanding example of research which bridges this gap. Hopefully, the research and modeling efforts on *H. zea* comprise an additional contribution, by illustrating how certain aspects of large-community composition of the ecosystem can be quantified in models of species populations. This is particularly well-illustrated in the model component representing the adult to egg flow, during which host preference mechanisms continually redistribute

the area population on many hosts, in many distinctly different, large community units within the agroecosystem matrix. During this redistribution, losses on one host are partially represented by gains on another. Thus, these intercommunity interchanges among population components and their natural enemies are of great significance in population dynamics and should be studied and modeled more effectively in the future.

This study also focuses attention on the important, but variable, role of an intrinsic regulatory mechanism (cannibalism) in not only regulating general population levels but in modifying temporal patterns of these levels. The intensity of cannibalism is influenced strongly by the number, nature, and relative attractiveness of feeding sites represented by the host plant matrix. Under North Carolina conditions, it is most intense on the most abundant and most attractive host plant (corn), and therefore has a major role in limiting general population levels there as well as in altering the temporal patterns of generation peaks. In other agricultural regions with different host plant complexes, cannibalism may not be as dominant in population regulation and population peaks may be more predictable on the basis of temperature-development data alone.

In the practical world of agriculture, decisions are made daily which could be better if the knowledge of the scientific community were synthesized more effectively for more confident predictions of pest populations. Obviously, predictions based on any model will be probabilistic because the complexity and open-endedness of the natural systems preclude perfect simulation. (A major difficulty is the poor predictability of the major driving variable, weather). However, a model such as ours, if used with caution, can be helpful in focusing attention on potential problems which might arise through the general adoption of revised crop mixes, no-tillage, double-cropping, new varieties with altered pest susceptibility, etc.

Although laced with rough approximations and an uncomfortably long list of assumptions, our modeling effort has already been useful in our efforts to improve agricultural pest control in North Carolina. The simple partitioning of soybean acreage into components on the basis of canopy development and fruiting in relation to moth flights has greatly simplified scouting and has contributed to more effective use of the threshold principle in applying insecticides. This required little new information on specific ecological factors and processes, but did require additional quantification and elucidation of their interrelationships.

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The Role of Pheromones in the Population Dynamics of the Western Pine Beetle

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ABSTRACT

Colonization of living trees by *Dendroctonus brevicomis* is characterized by a sequence of phases: dispersal, selection, concentration, and establishment. The concentration phase is initiated following release of the attractant pheromone, *exo*-brevicomin, and the host constituent, myrcene, by females feeding in the phloem. Maximum attraction occurs when frontalin is released by the male after entering the female entrance tunnel. Mixtures containing (1*R*,5*S*,7*R*)-(+)-*exo*-brevicomin and (1*SR*-)-frontalin are much more attractive than mixtures containing their antipodes. Only (+)-*exo*-brevicomin and (-)-frontalin are produced by the beetle. Mechanisms of pheromone biosynthesis recently described for *Ips paraconfusus* may also exist for the western pine beetle (WPB), e.g. the bacterium, *Bacillus cereus*, isolated from their hindguts synthesizes, *in vitro*, a pheromone component from α -pinene, a component of the host plant oleoresin. Verbenone, which is released by both male and female WPB, interrupts the attractant response of both sexes and thus may play a role in termination of the concentration phase. The principal insectan predators of the WPB arrive on the tree early in the concentration phase. These include *Aulonium longum*, *Enoclerus lecontei*, *Temnochila chlorodia*, and *Medetera aldrichii*. For *T. chlorodia* this behavior can be released by *exo*-brevicomin, and thus this pheromone component functions as a kairomone for this predator. In studies of behavior at and near sources of attractant pheromones, total catch is positively correlated with pheromone release rate. As release rate increases, beetles are caught at greater distances from the pheromone source. Also, a greater proportion of the beetles are trapped farther from the source. Analysis of the characteristics of the vegetative cover and topography around pheromone-baited traps indicates that slope and distance to the nearest ponderosa pine are negatively correlated with catch. The catch of WPB on traps baited with the mixture of *exo*-brevicomin, frontalin, and myrcene and attractive bolts cut from trees under attack is reduced greatly when the ternary pheromone mixture is released simultaneously from many stations around the attractant source. *exo*-Brevicomin released simultaneously from many stations reduces the catch on a trap baited with the ternary pheromone mixture but not on a trap baited with attractive bolts cut from trees under attack. The number of ponderosa pines killed by the WPB declines following a period when pheromones are released from traps to attract beetles over a 65 sq km forested area. Also, the proportion of WPB killed trees in the study area increases in areas with high trap density. This aggregation is interpreted to be a result of

population movement to areas of high pheromone concentration. A simulation modeling technique is being developed that will permit construction of models of population movement between individual trees in clusters and between clusters of killed trees. The outcome of this research has immediate practical implications for the use of behavioral chemicals in pest management systems.

To survive, the western pine beetle (WPB) invades living trees and only after death of the tree is assured does food become available for the WPB progeny. This insect has evolved a complex behavioral system to accomplish the "coup de grace."

In 1931, Person formulated a hypothesis that was to become the theoretical foundation for the subsequent highly productive experimental work on bark beetle pheromones. He proposed that *Dendroctonus brevicomis* LeConte was attracted to susceptible ponderosa pines (*Pinus ponderosa* Lawson) by "... the formation and escape of the volatile aldehydes or esters which are a by-product of a respiratory fermentation resulting from abnormal enzyme activity in subnormal trees ... After a few attacks are made, a second, stronger attraction is started by yeasts introduced by the attacking beetles. This secondary attraction is probably strong enough to attract beetles for a considerable distance with the result that the tree is usually heavily attacked and killed." That part of the theory referring to "secondary attraction" has been subsequently designated by most investigators as the bark beetle attractant or aggregation pheromone system. The chemical basis of this aggregation behavior described by Person was to remain a mystery until 1968 when Silverstein and his co-workers (Silverstein et al. 1968) identified a unique bicyclic ketal, *exo*-brevicomin (*exo*-7-ethyl-5-methyl-7,8-dioxabicyclo(3.2.1.)octane), as the principal attractant in frass produced by females boring in ponderosa pine.

Secondary attraction appears to be a common phenomenon throughout the Scolytidae (Borden 1974, Lanier and Burkholder 1974). Many species have evolved the capability to exploit trees weakened or killed by other bark beetle species, by other insect species, and by other destructive agents. Between 1931, when Person's paper was published, and May 1975, Borden et al. (1975) list 309 papers describing various aspects of the secondary attraction phenomenon. All but three of these papers have been published since 1960. Silverstein et al. in 1966, identified ipsenol ((-)-2-methyl-6-methylene-7-octen-4-ol), (+)-*cis*-verbenol and ipsdienol ((+)-2-methyl-6-methylene-2,7-octadien-4-ol), as attractant pheromones produced by male *Ips paraconfusus* Lanier. Since then, attractant pheromones have been identified from, and/or shown to attract over 17 species of Scolytidae from the genera *Dendroctonus* Erichson, *Gnathotrichus* Eichhoff, *Ips* DeGeer, *Orthotomicus* Ferrari, and *Scolytus* Mueller (Borden et al. 1975). These compounds are active both alone and in a great variety of mixtures. In addition, verbenone, *trans*-verbenol, ipsdienol, and 3-methyl-2-cyclohexen-1-one (MCH), all of which have been identified from bark beetles, have been shown to interrupt the attractant response of several species to their pheromones. The studies reported here on the WPB offer insight into the role of pheromones in the population dynamics of other Scolytidae.

The host colonization behavior of bark beetles that kill living trees has been characterized by four major phases: dispersal, selection, concentration, and establishment (Wood 1972, Borden 1974). The dispersal phase begins with emergence from the brood tree and ends with a response to host stimuli and/or attractant pheromones (Wood 1972). The selection phase begins with a response to host stimuli prior to, and/or after, landing on the tree, and ends with sustained feeding in the phloem. The concentration phase begins with response to attractant pheromones that are produced by females feeding in the phloem, the release of host compounds, and/or other processes. The establishment phase is initiated at some optimum attack rate and density where sufficient fungal inoculum has been introduced into the xylem to overcome tree resistance, so that mating, gallery elongation, and oviposition can proceed. The concentration phase continues beyond the attack density required to kill the tree as a result of continued production of attractant pheromones. Termination of the concentration phase occurs prior to sustained feeding, which results in no further pheromone production. Termination of the establishment phase occurs when elongation of egg galleries and oviposition cease. Attractant pheromones can be produced by some species when forced to feed in the non-host (Jantz and Rudinsky 1965, Wood et al. 1966). Also, the WPB will land on non-hosts, (Wood et al. unpublished data). However, non-host trees are not colonized by these species, indicating that sustained feeding does not occur. This may be due to the absence of feeding stimuli or the presence of feeding deterrents.

Survival of the beetle population or the tree is a result of the complex interactions among the WPB population, the vectored microorganisms, the physico-chemical properties of the host, and

predators, all influenced by the vagaries of the physical environment. Pheromones are the key mediators of the concentration phase. Failure to kill the tree during the concentration phase results in beetle mortality. In this paper, we summarize the research that elucidates, in part, the mechanisms governing the behavior of individuals, both WPB and its natural enemies, during the concentration and establishment phases, and the significance of this behavior at the population level.

The Olfactory Stimuli

Several important discoveries laid the foundation for isolation and identification of the WPB attractant pheromone. Anderson in 1948 determined that when recently cut jack pine (*Pinus banksiana* Lambert) logs were confined with newly emerged male *I. pini* (Say), the resultant attacks were attractive to males and females, whereas logs with boring females and logs alone were not attractive to beetles of either sex. Wood and Vite in 1961 quantified the secondary attraction phenomenon for *I. paraconfusus* by monitoring a cut tree under natural attack, including the initial, mass, and terminal components of the concentration phase. They also demonstrated that only the male, excavating entrance tunnels in the host, elicited this attractant response while the females did not. In 1962, this secondary attraction was proved to be a result of olfactory, not acoustical or visual stimuli in both field (Vite and Gara 1962) and laboratory assays (Wood 1962, Wood and Bushing 1963). These air-borne stimuli were discovered to emanate from male frass (a mixture of fecal material and phloem and xylem fragments) and to elicit an upwind walking response in the laboratory olfactometer (Wood 1962, Wood and Bushing 1963). Silverstein et al. (1966), using microchemical techniques and the above laboratory assay (Wood et al. 1966), isolated and identified three compounds from male frass that were inactive individually, but together duplicated the response to frass and to male-infested ponderosa pine. These compounds were shown to be attractive in the field to flying beetles of both sexes (Wood et al. 1968), thus demonstrating the close relationship between the attractant behavior of walking and flying insects.

Using this knowledge of the chemosensory behavior of *I. paraconfusus*, under both laboratory and field conditions, and the techniques developed to isolate and identify biologically active compounds that occur in small amounts, Silverstein et al. (1968) identified *exo*-brevicomin and myrcene (Silverstein 1970) from frass produced by female WPB. *exo*-Brevicomin was attractive to both sexes in the laboratory. Myrcene, a constituent of ponderosa pine oleoresin, was inactive alone but synergized the attractant response to *exo*-brevicomin. Bedard et al. (1969) demonstrated this same pattern of activity under field conditions. Renwick and Vite (1968) isolated *trans*-verbenol from female and verbenone from male WPB hindguts, although no behavioral role was indicated for these compounds. Kinzer et al. (1969) isolated and identified frontalin (1,5-dimethyl-6,8-dioxabicyclo (3.3.1)octane) from hindguts of male WPB.

Vite and Pitman (1969) indicated a male role in pheromone production when they discovered that the mixture of *exo*-brevicomin, frontalin, and oleoresin from ponderosa pine was the most attractive mixture to WPB in flight. This discovery was verified by Bedard et al. (1970) who, in addition, showed that myrcene accounted for most of the activity in oleoresin. In both of these studies, the sex ratio of trapped beetles was 1:0.4 male/female when exposed to binary mixtures containing *exo*-brevicomin and host-produced compounds, and was 1:2.6 when exposed to frontalin and host oleoresin (Vite and Pitman 1969). In addition to greatly increased catches, the sex-ratio was shifted to 1:1 when ternary mixtures containing both *exo*-brevicomin and frontalin with either oleoresin or myrcene were presented. Recently, we (Wood et al. 1976) have demonstrated that males and females are attracted to ternary mixtures containing (1*R*,5*S*,7*R*)-(+)-*exo*-brevicomin and (1*S*,5*R*)-(-)-frontalin and myrcene. Response to these mixtures in which the antipodes were substituted was greatly reduced. Stewart et al. (1976) has determined that only (+)-*exo*-brevicomin is present in cold trap condensates of aerated ponderosa pine logs infested with female WPB, and only (-)-frontalin is present in hindguts of the males. Only the enantiomers that occur in the beetles appear to be active, at least at the concentrations tested.

Recent studies have indicated some mechanisms of pheromone biosynthesis in bark beetles. Adult *I. paraconfusus* exposed to (-)- α -pinene vapor produced (+)-*cis*-verbenol in the hindgut while those aerated with (+)- α -pinene produced (+)-*trans*-verbenol (Renwick et al. 1976). *Cis*-verbenol is one of three components of the *I. paraconfusus* pheromone and both enantiomers of α -pinene are found in ponderosa pine (Goldblatt 1952), a host of this bark beetle species. Further, Brand et al. (1975) demonstrated that *Bacillus cereus* (Frankland and Frankland) isolated from guts of both male

and female *I. paraconfusus*, could synthesize both *cis*- and *trans*-verbenol from α -pinene *in vitro*. Hughes (1973) exposed WPB females to α -pinene vapor and observed increased amounts of *trans*-verbenol in the hindgut. However, *trans*-verbenol does not appear to be part of the WPB attractant pheromone (Bedard et al., unpublished data). Recently, Brand et al. (1976) have shown that a symbiotic fungus present in the mycangium of the female southern pine beetle (*D. frontalis* Zimmerman), a close relative of the WPB, can oxidize both *cis*- and *trans*-verbenol to verbenone. As with *trans*-verbenol, verbenone does not appear to be part of the attractant pheromone of this species, nor of the WPB (Bedard et al. unpublished data), but is an anti-attractant for the WPB (Renwick and Vite 1970, Bedard et al. in Wood 1972). Nevertheless, the activity of these microorganisms found in the gut and in the highly specialized, sex-specific, integumentary mycangium are promising leads in determining the mechanisms of pheromone biosynthesis. In addition to these bacteria and fungi, Person (1931) hypothesized that yeasts might produce these attractants. Since yeasts are found in the mycangium (and probably in the gut) of both WPB (Whitney and Cobb 1972) and *D. frontalis* (Barras and Perry 1972), they remain a promising source for the synthesis of these compounds.

Flight Behavior

A. Role of the Sexes in Concentration

The discovery that male-produced frontalin enhanced the activity of both *exo*-brevicomin and oleoresin (Vite and Pitman 1969) and *exo*-brevicomin and myrcene (Bedard et al. 1970) stimulated investigation of the concentration phase of the WPB on trees under attack. Only the males of *I. paraconfusus* boring in the phloem produce pheromones which concentrate the population (Wood and Vite 1961). Thus, it was assumed that the sex initiating the entrance tunnel into the bark was responsible for producing the attractant pheromones. Vite and Gara (1962) had trapped both sexes of the WPB in response to ponderosa pine bolts infested with females. However, field studies by Bedard et al. (unpublished data) demonstrated that when males were added to bolts infested with females, the mean catch was greatly increased over bolts infested with females alone. To initiate the concentration phase, trees were baited for one day with a mixture of *exo*-brevicomin, frontalin, and myrcene. After 1, 4, and 9 days, they were felled and alternate bolts either assayed for attraction or dissected. The most attractive bolts were from trees felled one day after baiting. The dissected bolts contained female galleries mostly less than 2 cm long and half of the galleries contained males. Bolts from trees 4 and 9 days after baiting were much less attractive and the female galleries were much greater than 2 cm in length, and most contained males. These results indicate that the male component of the WPB pheromone is released shortly after entering a recently excavated female entrance tunnel.

In laboratory studies, Browne et al. (unpublished data) identified *exo*-brevicomin and myrcene in cold-trap condensates of aerated, female-infested bolts. When males were permitted to enter the galleries, frontalin, which was not present earlier, was identified in the condensates, thus providing evidence for the chemical basis of the attraction behavior observed by Bedard et al. on trees under attack.

B. Termination of the Concentration Phase

Verbenone has been found to interrupt attractant activity (Renwick and Vite 1970, Bedard et al. in Wood 1972). Renwick and Vite (1970) have postulated that verbenone which is released by males inhibits further response on a tree or a portion of a tree. However, attraction to a tree under attack has been observed to continue for 8 days at a relatively high level, i.e., mean catch of 209 beetles/day/6 sq. ft. of trapping surface after the bait was removed (Bedard et al., unpublished data). Recently, Stephen and Dahlsten (1976a) trapped WPB for 15 days on ponderosa pines baited with either frontalin or female-infested bolts. Following this period, they did not separate emerging parent adults from beetles arriving on the tree. After 60 days, they assumed that the beetles on the traps were emerging new brood adults. Miller and Keen (1960) report that parent adult emergence does not occur until the new brood reaches the mid-larval stage, probably a period of 20-30 days following attack. Further, Browne et al. (unpublished data) have found verbenone and frontalin in the air around female-infested logs following the introduction of males, and equal amounts of verbenone in

the air around logs infested with females alone. Bedard et al. (unpublished data) have shown that the highest level of attraction during the concentration phase occurs when males join recently initiated female galleries. Thus, the simultaneous release of the anti-attractant verbenone, and the attractant frontalin, by the male during a period of maximum attraction, may be a result of the relative and/or absolute concentration of these compounds released during the mass attack period, and probably varies through time on different parts of the tree. Also, other compounds may play a role in termination of the concentration phase.

Although interruption of the attractant response by sonic communication has not been demonstrated for the WPB, it may play a role in the termination of the concentration phase of this species. Rudinsky and Michael (1972) have shown that stridulation by male *D. pseudotsugae* Hopkins was stimulated by volatiles from female frass as well as by components of the ternary pheromone mixture, i.e., frontalin, 3-methyl-2-cyclohex-1-one (MCH), and *trans*-verbenol. The female response to this male-produced sound was to "negate" the attractant pheromone through the release of larger amounts of MCH, which Rudinsky et al. (1973), termed a pheromone "mask" or "anti-aggregative" pheromone. Thus, MCH appears to be an attractant pheromone at low concentration and a "mask" at high concentration.

In addition to the production of various anti-attractants described above, termination of the concentration phase is probably influenced by the production of pheromones on adjacent trees, behavioral interactions among arriving beetles and beetles present in entrance tunnels, predation, and depletion of the population of attacking beetles.

C. Response of Associated Insects

(1) Natural Enemies. — Bedard et al. (1969) demonstrated that both female-infested bolts of ponderosa pine and *exo*-brevicommin were attractive to both sexes of *Temnochila chlorodia* (Mannerheim) (Coleoptera: Trogostidae). Pitman and Vite (1971) also recorded high catches of this predator in response to *exo*-brevicommin. Thus, *exo*-brevicommin functions as a kairomone. Predator survival is enhanced because they aggregate on trees under attack, while high densities of adult WPB are available for food. Also an adult bark beetle meal appears to be a necessary requirement for gametogenesis in this predator.¹ Following mating, oviposition, and eclosion, the larvae enter the bark beetle galleries to prey upon immature bark beetles. Because this predator has a very large host range (Struble 1942), it probably responds to components of the pheromones of many bark beetle species.

Stephen and Dahlsten (1976b) have determined the arrival patterns of some 100 species of insectan associates of the WPB, from the period prior to initiation of the concentration phase, to emergence of the new brood. The principal predators of the WPB began arriving early in the concentration phase and arrived in the greatest numbers during this phase. These predators were *Enoclerus lecontei* (Wolcott) (Coleoptera: Cleridae), *T. chlorodia* *Aulonium longum* LeConte (Coleoptera: Colydiidae), and *Medetera aldrichii* Wheeler (Diptera: Dolichopodidae). The catch of *E. lecontei* continued beyond the establishment phase and they were observed feeding on WPB adults, presumably emerging parent adults. The parasites, *Roptrocercus xylophagorum* (Ratzeburg) (Hymenoptera: Torymidae) and *Dinotiscus burkei* (Crawford) (Hymenoptera: Pteromalidae), arrive during late larval development of the WPB. Clerids have been observed only occasionally on traps baited with *exo*-brevicommin, frontalin, and myrcene. However, we (Wood et al. 1968) have trapped *E. lecontei* in response to synthetic attractant pheromones of *I. paraconfusus*. These studies indicate that the success of the concentration phase may be influenced by the rate of predation on attacking WPB (Wood 1972).

(2) Other Bark Beetle Species. — Bark beetle species that invade living trees frequently occupy different portions of the tree both simultaneously and in some predictable sequence. In WPB-killed trees, *I. paraconfusus* (Struble and Hall 1955) and *I. pini* (Miller and Keen 1960) colonize the upper

¹ T.B. O'Connell. 1967. Laboratory studies of the predaceous beetle, *Temnochila virescens chlorodia* (Mannerheim) (Coleoptera: Ostomidae) with emphasis on continuous rearing. Ph.D. Dissertation, University of California, Berkeley, 92 pp.

portion of the bole, mostly in the crown. These insects are found in about the same stage of development together with WPB, but little is known about their colonization behavior in living trees under attack by WPB. However, recent work (Birch and Wood 1975) has demonstrated pheromone-mediated interactions between two species of *Ips* that cohabit the same host trees. Male-produced volatiles from *I. paraconfusus* interrupt the attractant response of *I. pini* to *I. pini* pheromones and vice versa. This interruption of the *I. pini* attractant response can be duplicated by ipsenol, a component of the *I. paraconfusus* pheromone. In a follow-up to this study, Byers et al. (unpublished data) have shown that bolts infested with *I. paraconfusus* interrupt the response of the WPB to attractive bolts cut from trees under attack by WPB. These studies indicate that interspecific pheromone interactions may explain in part the spatial and temporal relationships among bark beetles on the same host tree.

D. Behavior Near a Pheromone Source

The attractant behavior of WPB at and up to 18 m distant from a synthetic pheromone source has been studied in several field experiments.² Sticky traps were hung at 1.5 and 5.2 m on tree trunk-simulating silhouettes (6 m in height) at 3, 9, and 18 m from a small sticky basket trap, from which *exo*-brevicommin (E), frontalin (F), and myrcene (M) were released. Generally, as the release rate increased, total catch increased. At higher release rates, a greater proportion of the beetles were trapped further from the source. Also, as pheromone release rate increased beetles were caught at greater distances from the pheromone source. As pheromone release rate was increased from 2-20 mg (E:F:M)/compound/24 hrs., the total catch at all positions, except at one height 18 m from the source, also increased. Increasing the release rate from 20-200, increased the total catch three-fold, but increased the proportion of the total caught at 9 and 18 m from the source. Also, the catch at the release point was less than that observed for lower release rates. At a release rate of 2:2:20 or 20:20:2 for E:F:M, the catch was only 1/5 that caught at a 20:20:20 release rate. The catch at a release rate of 2:20:20 was not different from that recorded at a release rate of 20:20:20 for E:F:M.

E. Interruption of the Attractant Response

(1) Attractant pheromones. — In an experiment similar to one performed by Gaston et al. (1967) and Shorey et al. (1967), plots 0.81 hectare (90 x 90 m) in size were established in ponderosa pine stands. An attractive bolt cut from ponderosa pines under attack, or a 1:1:1 ternary mixture of E:F:M was placed in the center of the plot. E, F, and M, individually and in a ternary mixture, were released at various rates from 48 stations 15 m apart in a 7x7 grid. A measure of interruption was obtained by comparing the daily catch on the centrally-located trap before, during, and after pheromones were released at the grid stations. In one experiment the ternary mixture was released at each grid station at a rate of 1 mg/compound/16 hrs. The catch on the centrally-located trap baited with the ternary mixture released at the same rate, was reduced by 97% compared to the catch on the same baited trap on days when no compounds were released from the grid stations. Similarly, *exo*-brevicommin alone released from the grid stations reduced the catch by 89%; myrcene reduced it by 51%; but frontalin increased the catch 23%.

In another experiment, *exo*-brevicommin released alone from the grid stations only slightly reduced the catch on the center trap when it contained an attractive bolt, while the ternary mixture greatly reduced the catch on the center trap, i.e., 14% vs. 94%. Again, both the ternary mixture and *exo*-brevicommin alone greatly reduced the catch on the center pheromone trap when it contained the ternary mixture, i.e., 95% and 85% respectively. Because EFM lowers the catch at attractive bolts and E alone does not, we believe that synergism among these compounds is required to obtain interruption. Also, because E lowers the catch on traps baited with EFM but not on traps containing attractive bolts, EFM may not be a complete pheromone mixture. However, differences in relative and absolute concentrations of these compounds may also account for the results obtained.

(2) Anti-attractants. — Verbenone and *trans*-verbenol released with EFM result in lowered catches when compared with EFM alone (Bedard et al. unpublished data). Verbenone, released at 4

² P.E. Tilden. 1976. Behavior of *Dendroctonus brevicomis* near sources of synthetic pheromones in the field. M.S. Thesis, University of California, Berkeley, 66 pp.

mg/24 hrs. at the mid-point of an attractive bolt, reduced the catch 86-95% over bolts from the same tree without verbenone.

F. Influence of Synthetic Pheromones on the Level and Distribution of WPB Populations

Further insight into the population dynamics of this beetle has been obtained in field studies aimed at selective reduction of adult WPB populations over a 65 sq km forested area (Bedard and Wood 1974). Traps with about 6 sq m of sticky screen panels were erected on 0.8 km centers over the entire study area, and on 161 m centers in four 1.3 sq km plots. Also, two check plots, each 2.56 sq km, were established. The traps were baited with EFM and these compounds were evaporated at a rate of 2 mg each/day in the 0.8 km grid and 20 mg each/day in the 161 m grids. Traps in the four plots were in place during April-June (1970), the period of emergence of the overwintering population. Traps in the 0.8 km grid were in place from May to October. Tree mortality and attack and emergence densities were estimated before, during, and after the experiment.

DeMars et al. (unpublished data) estimated that the number of ponderosa pines killed by WPB declined from a total of 283 ± 94 trees overwintering in 1969/70 prior to exposure to pheromone baited traps, to 91 ± 28 trees overwintering in 1970/71. Also the pheromone treatment affected the distribution of WPB-killed trees (Bedard et al., unpublished data). Prior to treatment, the proportion of all WPB-infested trees in the study area was equal in the four plots containing attractant-baited traps on 161 m centers, and in the two check plots, i.e., 8.6% in each area. However, during the April-June period, the proportion of WPB-infested trees increased in the four plots to 18.8% compared to 8.0% in the check plots. We interpret this to be a result of population movement to areas of high pheromone concentration, i.e., 1.32 gm of each compound per day per 1.3 sq km plot. In the year following the treatment, the infested trees were more equally distributed among the two check plots and the four plots that had contained attractant-baited traps, i.e., 10.2% and 13.3%, respectively. However, these percentages represent only a few WPB-infested trees i.e., an aggregate of 49 ± 18 for two generations.

The catch on the 99 attractant-baited traps on 0.8 km centers (2 mg each/24 hrs of EFM) was monitored throughout the flight season of the WPB as part of the experiment described above (Bedard et al., unpublished). Features of trap site such as, vegetation, topography, and WPB local abundance were analyzed for association with trap catch for each of three periods corresponding to WPB generations. Trap catch was negatively correlated with slope and distance to the nearest ponderosa pine. The catch on most traps, relative to the total catch during each period was fairly consistent for the three periods. Catch was not significantly correlated with estimated local WPB abundance.

These results suggest that beetles may fly some distance from their origins and concentrate in highly attractive centers, and that during flight, they exhibit a preference for ponderosa pine stands on more level terrain.

Population Models

Ewing et al. (1974) have presented a progress report on the development of a modeling technique which simulates the dynamics and structure of a biological population. The technique is a discrete, stochastic simulation of biological processes, which allows input from continuous processes. The technique simulates the dynamics of a given population by accounting for the dynamics of individuals within that population. Mathematically, it is a Monte Carlo process, which subsamples the set of all possible paths through the state space in order to stimulate the dynamics and state of the population. Monte Carlo processes are dependent upon the quantity and quality of the incoming data that are used to generate the empirical distribution functions. To model the dynamics of the western pine beetle/ponderosa pine system, we have decomposed this system into a network of models that overlap in time and space. Each model spans about 10^4 , both in area and time, and communicates with adjacent models through the region of space-time overlap. Simulation models of the following biological processes will be required³:

³Wood, D.L. Progress Reports, Pine Bark Beetle Subproject, *In* "The Principles, strategies, and tactics of pest population regulation and control in major crop ecosystems," Vol. 1, 1973, and Vol. 2, 1975.

(1) The behavior of the WPB flying near ponderosa pine and other objects such as synthetic pheromone-baited survey and suppression traps and trunk simulating silhouettes: Here an effort will be made to explain the behavior of the WPB taking off from, flying near, or landing on ponderosa pines or other trees species or traps under the influence of attractant pheromones and other behavior-modifying chemicals.

(2) The relationships between WPB and individual ponderosa pines killed by WPB both within and among clusters: Some of the processes to be considered are the rates of attack and emergence of beetles from individual trees, rates of predation, the rate of movement of the beetles into and out of a cluster, and the initiation of new clusters. Some of the events are: the initiation and location of beetle attack on, and emergence from, ponderosa pines. For these models, we have the following detailed information from a 140 sq km forested area: the distribution and abundance of WPB-caused tree mortality over a four-year period, WPB attack and emergence densities for the same period, and weekly catches of WPB for two years on traps located on 0.8 km centers. Presently we are preparing these data for analysis. Through these models we hope to design better field experiments to help us further unravel the complex role of pheromones in the population dynamics of bark beetles.

Conclusions

Since the early 1900's, a very large research effort has been focused on the population dynamics of the western pine beetle. In their book "Biology and Control of the Western Pine Beetle", Miller and Keen summarize the work on this insect during the 50 years prior to 1960. This early research was concerned primarily with the population dynamics of the WPB in old-growth ponderosa pine forests, while subsequent studies by Stark and co-workers (Stark and Dahlsten 1970) have been conducted in second-growth forests. Most of this earlier research has emphasized within-tree dynamics. The succession of organisms following the establishment phase of host colonization, through emergence of the new brood adults, is both dynamic and extremely complex. However, no matter how well we understand within-tree population dynamics, prediction of population size in the next generation will not be possible until we can estimate the quantitative relationships between mortality occurring within the tree prior to emergence, and the mortality occurring between emergence and successful colonization. The problems in obtaining total, adult population estimates of the WPB result from its high mobility, highly aggregated distribution, multivoltinism, and capacity to produce more than one brood. About one-half of the attacking population emerges from the killed tree to attack other trees (Miller and Keen 1960). Perhaps some individuals are even capable of attacking a third tree. In other words, we need a complete account of generation mortality before we can intelligently establish priorities for further work on a particular life stage and/or mortality agent or process. Certainly, the studies that are possible in the WPB system are inexhaustible. Stark (1970) summarized the significance of the biology of adults between emergence and the establishment phase as follows: "Little is known of the flight habits of the western pine beetle, or of its behavior prior to the establishment of successful attacks. Certainly, the period from first emergence . . . (and second or third) . . . to appearance on a new host tree is one of the most critical of the life cycle. The adults are exposed to a completely different environment from the immature stages, and are subject to all the vagaries of climate and associates in their ecosystem." Identification of the attractant pheromones of the WPB has opened up a new era in the investigation of WPB population dynamics, namely the biology of adults during the dispersal, selection, concentration, and establishment phases of host colonization. Attractant pheromones used over large areas have potential for estimating the size and distribution of WPB populations, and for manipulating populations as a means of determining the interactions of adult WPB populations with its host and natural enemies. Further, these attractants can be used experimentally to redistribute populations so that we can study the dynamics of population behavior. At the same time, we can expect that the outcome of this research will have immediate practical applications for the use of behavioral chemicals in pest management systems.

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Section 11: Forest Entomology

Insect Impacts on the Quality of Forest and Urban Environments

Organizer: William E. Miller (USA)

Convener: William E. Waters (USA)

Insect Impact on the Quality of Forest and Urban Environments: The Biological Viewpoint

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ABSTRACT

The impact of insects on the quality of forest and urban environment manifests itself, from the viewpoint of man, in an either direct or indirect way. In the first case, the deterioration of the environment is due to the mere presence of some annoying or aggressive insects which, however, do not change the forest ecosystem. In the second case, the insects attack and injure the forest, and in this way cause more or less radical changes of the environment.

Under "normal" conditions, i.e., in a healthy and site-adapted stand and favourable weather, the insect impact on the environment is generally limited. The biological balance of the forest is, however, very labile and is easily disturbed due to changes of the climate, natural catastrophies, or activities of man. After such disturbances the environmental resistance is reduced and outbreaks of forest pests with following changes of the environment take place. Modern silvicultural measures to a large extent promote pests by providing excellent conditions for their development and multiplication.

The Organizing Committee of the Forest Entomology Section has kindly invited me to speak to the Congress about "Insect Impact on the Quality of Forest and Urban Environments," with special emphasis on the biological viewpoint. It is a very flattering commission and a great privilege to speak to this select audience.

I have certain doubts, however, whether my paper will satisfy the colleagues from all parts of the world as my experience regarding this subject derives from a rather limited geographical area, namely Northern and Central Europe. My knowledge of insect impacts on urban environment is, furthermore, poor and lies outside my field of competence. Another disadvantage might be that my English may turn out to be not fully comprehensible to the audience.

In order to prevent potential misunderstandings, I would like to make some explanations and distinctions relating to the subject of the lecture. First of all, the insects of the title are here interpreted as forest insects, i.e., not only pests, but all insect species living in forest environments. "Forest environments" apply here to forest stands generally, including forest soil and existing local climate. The term "urban environment" refers to all "green areas" within or in the vicinity of cities or other communities, i.e., areas covered with shade and ornamental trees, or in other words, parks, avenues, and other places where trees grow.

I would like, furthermore, to stress that the subject of this paper is very extensive; it would be sufficient for a series of lectures. For that reason I cannot be expected to give an exhaustive account on this subject.

The forest insects are generally classified into three ecological groups: (1) harmful species which cause measurable losses to living trees or forest products, (2) useful species (parasites and predators) which are enemies of forest pests, and (3) indifferent species which make the bulk of the forest fauna. This classification is not quite acceptable, especially as regards the indifferent species. The major part of these species consists of various kinds of wood eaters which contribute to the

decomposition of wood or act as humus producers. All these species also produce nitrogenous material in the form of excrements. They should consequently be regarded as beneficial species.

When speaking about the impacts of insects on the quality of forest and urban environments from the viewpoint of man, one has to make a distinction between direct and indirect impacts. In the first case it is a question of immediate effect on the environment owing to the unpleasantness and offensive behavior which certain insects cause by their activities and in this way deteriorate the environment. In the latter case the impact of the insects is directed against the forest and consequently also against the environment, including man.

In order to illustrate the immediate impact, several examples can be given. Caterpillars of Processionary bombycids (fam. *Thaumetopoeidae*) and of the moth *Euproctis chrysorrhoea* L. have so-called "poisonous hairs", which easily break and by contact with human skin, and especially with mucous membranes, cause eczema and inflammations. Mass outbreaks of the Pine processionary moth, *Thaumetopoea pinivora* Tr., on the south coast of the Baltic sea have caused a depopulation and closing down of several seaside resorts.

Another moth species, Mountain birch looper, *Oporinia autumnata* Bkh usually occurs periodically in enormous numbers over extensive areas in North European mountain regions and defoliate the Mountain birch (*Betula tortuosa*). From the forestry point of view these injuries are of less importance, as this birch is used for fuel only. The consequences to the private economy, however, are considerable. Hotels and youth hostels are usually deserted during outbreaks which go on for several years, owing to the ubiquitous larvae which also ruin clothes, soil the food, and spread a nasty smell. Also, for anglers the *Oporinia*-outbreaks are synonymous with bad years because the fishes are satiated and do not take other offerings. Inconveniences such as these are especially noticeable in parks, gardens, and garden restaurants in towns or suburbs. Shade trees are here exposed to outbreaks of various kinds of defoliators, chiefly larvae of the Oak leaf roller (*Tortrix viridana* L.), the Winter moth (*Operophtera brumata* L.), etc. Visits to such places may be unpleasant on account of the excrements falling down and numerous caterpillars spinning down and crawling about.

Of insects belonging to this category are also many other nasty species, sometimes injurious to the health, which can spoil forest and urban environment so badly that the infested places become, at least temporarily, deserted. Midges, gnats, gadflies, wasps, ticks, flies, etc., belong to this category. Some of these insects may even cause economic losses. By means of time studies at the construction of power plants in well-forested regions in Northern Sweden, it has been possible to establish that 10-15% of the work time was used by the workers to killing mosquitoes.

As a general statement of the direct impacts of insects on man, it can be said that these cause considerable deterioration of the environment, often resulting in economic losses, but that the changes are temporary and in many cases the inconvenience and the unpleasantness may be lessened or eliminated by means of simple preventive remedies (for example insect repellants, etc.).

The indirect impacts on the environment caused by forest insects while attacking and devastating forest stands are more severe and longer lasting. These impacts occur, however, only under certain conditions.

In a normal and healthy forest with site-adapted tree species and provenances, and consequently strong resistance, the biological balance prevails. Such forests over time generally counteract or withstand outbreaks of the aggressive insects. The impact on forest and forest environment does not take place until the biological balance for some reason or other is disturbed, whereby the environmental resistance drops to a low level. I will return to the nature of these disturbances and to the origin of insect calamities later on. Now I would like to give a short survey of the ways in which insect pests injure the forest, and thus affect the forest environment.

As we all know, most forest insects cause damage to living trees by eating needles and leaves, buds and shoots, cones and seeds, bark, phloem and roots. They also attack lying trees and parts of trees. Other species live in the wood on both standing and lying trees and form the rather extensive group of wood destroyers. Another group of insects specialize as transmitters of plant diseases. Some insects on account of their mode of life are able to belong to different groups. In the *Monochamus* species, for example, the larvae are wood borers, and the adults are bark eaters; the Pine shoot beetle, *Blatophagus minor* Hart., hollows out shoots as an adult and transmits blue stain fungi; its larva feeds on phloem.

Great damage and often of very severe kinds are caused by leaf- and needle-eating insects. In broadleaved forest the damage they cause is less dangerous. Even when the trees are completely defoliated, they shortly after form new leaves, and so the consequences will be increment losses only.

Far more dangerous are the devastations in coniferous forests. Pines generally survive one year of total defoliation, although not without losses. Two years of complete defoliation in a pine forest means total ruin. In spruce forests, complete defoliation is still more dangerous, since one year of such defoliation as a rule results in the death of the trees.

Luckily, such devastations do not occur very often in Northern Europe. During this century, only two great calamities of this kind have occurred in Sweden: one by the Nun moth, *Lymantria monacha* L., in spruce forests and one by the Pine noctuid, *Panolis flammea* Schiff., in pine forests.

Far more often, devastations occur by stem pests, of which bark beetles play the principal part. Such devastations usually flare up in connection with forest disturbances such as windfall, forest fires, dry and hot summers, etc., and continue for several years, in which case the infestation area gradually extends.

The damage caused by forest pests naturally affects the forest environment and, on the whole, proportionally to the extent of the damage. With total defoliation followed by clear cutting, the forest environment is most radically changed, because the stand of trees is gone and what is left is smaller vegetation, the forest soil with stumps and slash. With removal of the stand, the game also disappears. Other disadvantages from this kind of major disturbance are: covering with weeds, lowering of ground water level, impoverishment of the soil, increased evaporation, etc. On the credit side, the appearance of berry vegetation is worth observing, especially raspberries and cowberries which from the national economy point of view is of great value (one hectare clearfelled area with cowberries in the vicinity of towns in Sweden yields more a year in dollars than does one hectare of mature coniferous forest).

When the defoliation is only partial and not so widespread, and only a part of the stand is cut, lesser changes occur in the forest environment. Sparser canopy and more light and heat encourages the grass vegetation and in this connection also the game and domestic animals in countries where forest pasture is allowed. Water management of the soil is also better than on a clearfelled area. A negative factor is the impaired vigor of the remaining trees owing to the sudden exposure and consequently increased susceptibility to attacks by bark beetles, borers, etc.

In completely defoliated stands where no trees have been killed, the change in the environment (more light and heat) is only temporary, and the original environment is after a short time completely restored.

The impact on the urban and suburban environment is more marked for the town population on account of frequent visits to parks and uses of open-air recreation establishments. The growing conditions of trees in these establishments are usually poorer than those in the forest due to mechanical damage and pollution, (poisonous gases, dust, soot, etc.), which make them more susceptible to the attacks of insects. Many species of defoliators infest these parks and defoliate the trees. Wood destroyers (e.g., *Saperda*, *Cossus* et al.) are not uncommon in parks and avenues. The damage is often observed only after the stem has been broken by strong wind. Severe and irreparable damage has for many decades been inflicted upon elms in parks and avenues by attacks of Dutch elm disease, caused by a fungus (*Ceratocystis ulmi*) with different *Scolytus*-species as vectors. A great many old elms have been killed by this disease, which is difficult to control.

A phenomenon which recently has become noticeable in the vicinity of towns and suburbs is how some forest insects belonging to the group of wood destroyers migrate from the forest to buildings, especially holiday cabins situated close to the forest. Certain buprestids and especially carpenter ants (*Camponotus* species) cause great damage to these buildings. The frequency of these attacks is so great at present that some of the larger insurance companies include this damage in the general house insurance.

When determining the impact of forest insects on environment, one should not forget the beneficial species which form the major part of the forest fauna and by their activities contribute to the decimation of pests as well as to wood decomposition and humus formation. By doing this, they also contribute to the cumulation of plant nutrients and consequently to the improvement of the environment.

Even forest pests may contribute in a useful way from the excrements and dead bodies of the larvae during outbreaks which increase the nitrogenous nutrient in the soil. This can be observed in the ring growth of the remaining trees.

A question of great importance is how outbreaks of forest insects arise. The reasons for these can be classified into three groups: (1) outbreaks owing to the influence of the climate; (2) outbreaks as a result of natural catastrophies; and, (3) outbreaks as a result of the activities of man.

Influence of the Climate

This group includes the abiotic factors which favour the initial release and development of populations of forest pests. It is usually warm and dry summers that cause such outbreaks because of the impaired resistance of the trees and, often in combination, the increased fertility of the females of the insects. A certain connection between sunspot years and outbreaks with time intervals of about eleven years can be traced in certain insects.

Pests affected by climatic factors are mostly lepidopterous and hymenopterous leaf eaters which cause severe devastations of long duration over extensive areas. We are powerless to prevent outbreaks of these pests, as we cannot affect the climate. It is possible to reduce the extent of the damage however, if one avoids pure stands on large areas and cultivates tree species adapted to given climatic conditions.

Influence of Natural Catastrophies

Regarded as natural catastrophies are all kinds of calamities which happen to the forest and make it vulnerable to attacks by forest pests, i.e., windfall, snowbreak, avalanches, forest fire, flood damage and similar catastrophies. They have one thing in common from the forest insect point of view, and that is they produce abundant possibilities of breeding and development for a great number of different pests, of which bark beetles constitute the major part. The damage can be very severe and of long duration and has a tendency of spreading in various directions from the point of origin. Rapid measures are necessary, such as removal of timber and other suitable breeding material, or barking of logs and slash before bark beetle emergence.

Measures of Man

The third factor causing mass outbreaks of insect pests is the organism which calls itself *Homo sapiens*, a name not always rightly deserved in view of the well-being of the forest. Man is in this connection not homogenous, as his relationship to the forest varies greatly. Three main types of human viewpoint can be distinguished.

The first type is the silviculturist who, by taking measures, changes the environment of the forest and often causes outbreaks of various forest pests. At the same time he tries, by taking one or another suitable measure, to counteract these outbreaks. We can call this type *Homo sapiens* var. *forestalis*. The second type is the forest visitor who usually lives in towns, villages and other inhabited places and visits the forest for a long or short time during vacations. People who belong to this type visit the forest in order to rest and enjoy the peaceful nature. We can call him *Homo sapiens* var. *urbanus*. As regards interests, this group is very heterogeneous: besides nature lovers, it includes hunters, anglers, collectors (entomologists, ornithologists, botanists, et al.), artists, picnic people, sportsmen, etc., etc. A certain category of these people spend all their leisure time or the major part, in or in the vicinity of the forest and live in their own or rented villas, cabins or similar buildings. *Homo urbanus* is, from the forest protection point of view, fairly harmless but can through carelessness cause calamities such as forest fire. Certain fanatics of the *urbanus* type have a tendency to poke one's nose into forest management by making propaganda for "natural" silviculture, based chiefly on aesthetical viewpoints. They are as a rule uncompromising opponents of *all* chemical products which are used in the forest (i.e., insecticides, fungicides, herbicides and also fertilizer) and often disturb or sabotage the carrying through of the forest protection measures. These nature fanatics get their ideas from the press, the television and other mass media, well-known for spreading sensational and not always reliable information about the effect of chemicals on the forest.

The third type consists of the representatives of the authorities which regard the forest from the perspective of the writing-desk and create laws and regulations which are to be a standard for the continued existence of the forest. This type, which it would be appropriate to call *Homo sapiens* var. *bureaucraticus*, is distinguished by lack of biological knowledge and thinking.

When it comes to analyze the influence of man on the insect fauna of the forest, one must examine the activities of each of the various *Homo sapiens* types. The most important part is here naturally played by the silviculturist himself, because every interference in the life of the forest causes disturbances in the biological balance and, as a result of this, changes in the qualitative and quantitative composition of the fauna. Some insect species are promoted, some are suppressed.

Species belonging to those which are promoted are unfortunately severe pests. Each kind of cutting, such as cleaning, thinning, and final cutting, increases the breeding places of forest pests. Methods of reforestation can also cause the same effect.

The forest entomological consequences of silvicultural measures are inevitable, but it is possible to reduce their scope and seriousness. The constraint is, however, that the strategy of the silviculturist is in harmony with the principles of scientific forest protection or, in other words, when carrying out silvicultural measures, the greatest possible consideration should be given to the elementary demands of forest protection. This is the rational and pro-nature alpha and omega of forest management and at the same time the right way to avoid chronic insect damage in the forest. This question has many times been discussed all over the world at conferences, symposia and other professional meetings, at which forest biologists and ecologists have stressed the necessity of co-operation and co-ordination between silviculture and pest management.

Unfortunately, the development of forestry in practice has shown another trend which to a great extent has promoted pests and consequently intensified their impact on the forest environment. In order to exemplify this trend, I will give a brief account of forestry development in Sweden during the latest decades. First of all, it has to be stressed that the development of forestry is not a separate occurrence but an integrated process within the general national economy.

The reasons for the changes that have taken place are found in the constantly increasing labor costs which result in decreased net monetary returns, keen competition on the export market and so on. These factors force the forester to economize and rationalize the whole forest management process. Fundamental measures have been taken recently by changing silvicultural methods radically with the aim of reducing the costs as much as possible. Included in these measures are above all the mechanization of forest operations, the extension of cutting areas, the prolongation of thinning intervals and sometimes a total stoppage of thinnings, centralization of barking of pulpwood at pulp mills, etc.

All these changes may from the economic point of view be justified. From the biological, however, these measures are dangerous and unacceptable. The reason for this is that they promote the forest pests to a great extent and create excellent conditions for their outbreaks and higher levels of chronic damage in the forest. I can illustrate this with some examples. The mechanization, especially when it is a question of large logging machines, causes mechanical damage, above all to the forest soil with the result that the trees become susceptible to insect attacks. Large cutting areas cause drying up and deterioration of the soil because of weed covering, erosion and impoverishment, whereby the artificial regeneration is made more difficult and the vigor and resistance of the plants are impaired. The large cutting areas have furthermore caused mass propagations of forest insects which up to now have been unknown as pests, for instance, the sawfly species, *Diprion pallipes* Fall. which to a great extent attacks and kills young plants of Scotch pine. Large cutting areas act as magnetic fields and cause influx and concentration of insect pests which breed in tree stumps and roots or in slash. Several of these insects attack cultivated plants in the cutting areas, especially coniferous plants which to a great extent are damaged or killed.

In regard to the reduction in frequency of thinnings, this measure increases the risk of spreading of insects from dying to living trees. The barking of pulpwood only at the pulp mills has resulted in the leaving of unbarked pulpwood in the forest for several months or longer. This has greatly increased the mass production of bark beetles and borers. This applies especially to two bark beetle species, i.e., Spruce engraver, *Ips typographus* L., and the Pine shoot beetle, *Blastophagus piniperda* L. The former attacks and kills healthy trees of Norway spruce. The latter damages pines mainly by adult feeding in the shoots and causing great increment losses.

Before centralization of pulpwood barking had been introduced, the extent of the damage caused by *B. piniperda* has been comparatively limited. Nowadays the damage is considerable and extensive and the losses are estimated at many million dollars.

Changes in means of transport of cut trees have also taken place which promote forest insects and increase their impact on the forest environment. The earlier frequently used floating in Northern Europe has today, with few exceptions, been replaced by land transport. In this way the wood is much more exposed to attacks by insects and also blue-stain fungi.

Changes in forestry methods have also taken place regarding the time of cuttings. Earlier they were mainly concentrated in the winter season, and the timber was hauled out of the forest usually before the swarming of the insects. Today cutting is carried out all year round and the unbarked

timber has often to wait a long while for transport to a mill. When this occurs during the summer, the logs always are attacked by insects.

To sum up, modern methods of silviculture generally favor the multiplication of forest pests and the increase in numbers of otherwise harmless insects to damaging levels. The modern forester acts — often against his will — as the best ally and promoter of forest pests, and in that connection contributes in a very positive way to their impact on the quality of forest environments. Forest insects also receive a great help from the administrative and legislative quarters by regulations and prescriptions, which often counteract or make the control of forest insects impossible. As an example, I can mention the prohibition of the use of DDT for dipping of coniferous plants as a protective measure against attacks by Pine weevil, *Hylobius abietis*, the No. 1 enemy of these plants. Foresters have at present no other effective means against this pest and have to defenselessly watch the weevil destroy plantations, an activity which costs the Swedish forest industry between 200 and 300 million crowns (45-65 million dollars) yearly.

The above-outlined situations within forest protection illustrate the close connection between forest pests, the forest, and the activity of man. I have described primarily the conditions in Sweden, but these apply also to all of Northern Europe. The future prospects are gloomy because as long as man acts in the dark and completely ignores biological laws, the insects will to an ever-increasing extent devastate the forest, deteriorate its environment and perhaps play the leading part in the life of the forest.

The question will then be: What is there to do in a situation like this?

As we cannot influence the climate, nor prevent natural catastrophies, we ought to direct our ambitions, as has been pointed out earlier, to manage the forest in accordance with the chief principle of forest protection: Reduce the possibilities of development of forest pests in the forest to the utmost possible extent.

In order to reach this goal, objective information and a long-range perspective are necessary. Everyone who in one way or another comes into contact with the forest ought to have a clear perception that the forest is not only capital which yields interest, but is an ecological system with various living components in a very unstable balance that is extremely sensitive to interferences and disturbances which may cause devastation, which will have adverse impacts on the quality of the environment which he desires to maintain for his benefits.

Insect Impacts on the Quality of Forest and Urban Environments: The Economic Viewpoint

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ABSTRACT

Economics is useful in forest pest management because it can trace the effect of insect damage on the incomes of persons impacted. The major economic concepts underlying economic evaluations of insect management actions are reviewed, highlighting the differences between evaluations made from the private and the public point of view. Recent research in forest insect economics is reviewed, and a program of research combined with application is outlined.

Environment is a popular word these days, and environmental quality is a force abroad in the land. The environmental revolution is, of course, only the latest in a long series of painful adaptations our species is making — adaptations in attitude and action from man the predator and exploiter to man the participant and steward. Such changes do not come easily, or steadily, or everywhere at once. Often they come only, it seems, when there is no recourse — when it's clearly a case of adapt or die.

Each of us is most interested in his own personal environment — our home and place of work, our automobile and the roads we frequent, our family, friends and acquaintances. I've often thought that the place to start improving the environment is right in our own front parlors and back yards. Keith Arnold (1976) recently has written that "... our natural resources lie along a continuum which starts at the door of the high-rise apartment and extends to the heart of our wilderness areas." What happens in the forest influences urban environments, and the conditions of urban life certainly help determine how forests are used and abused.

Insects certainly do impact environmental quality. I invite anyone who doubts this statement to visit, say on a June day, any of the millions of acres of aspen-bracken fern, mosquito ecotype with which Michigan is so well endowed. As far as I'm concerned the mosquito is, without question, the most important of all forest insects. But I understand that I must limit my attention in this paper to insects that feed on trees and injure man only indirectly.

I'm going to begin by saying some general things about economics — about what it is and what it is not. Then I will discuss some of the concepts useful in establishing the economic dimension of insect impacts. Finally, I want to look at research and research needs in the economics of forest insect management.

I'm rather afraid that economics and economists have been given too high a place in the pantheon of worldly wisdom, at least until quite recently. Now we have books like Robert Lekachman's *Economists at Bay* (1976) to explain that economists are just as narrowly focused, and just as fond of ancient, honorable and somewhat incorrect theories, as any other body of specialists. Let me hasten to add that I am not particularly ashamed of being an economist, no more than I am of being a forester. Both disciplines embody some practical knowledge that is useful, if carefully applied in small doses.

Well, what is economics all about? And how, in particular, might it help us to understand more fully the impact of insects, whether in a forest or an urban setting? Economics is the study of wealth.

Indeed, the first great economics text, written exactly 200 years ago by Adam Smith, the Scottish professor of moral philosophy, is called *An Inquiry into the Nature and Causes of the Wealth of Nations*. Why are some nations wealthy, and others poor? What are the requisites of economic development? How is wealth used, and how is it shared? These were the questions which engaged Adam Smith's attention, and the attention of economists ever since. Not, one might say, with overwhelming success, judging by the generally impoverished condition of the majority of the human species.

The economist, then, is primarily interested in one facet of the human condition — material wealth or well-being. And the economist's stock in trade is his ability to predict how, and to what extent, the material well-being of impacted individuals and groups will be influenced by a contemplated action — an action like an oil embargo, price control legislation, the construction of a new steel mill, or even a spruce budworm control project.

It is at this point that I wish to stress what economics is not. Economics is not esthetics, politics or ethics; and all of these may play a role in our final decisions about insect management or any other human activity. An insect may be causing great losses in income and wealth. And a control action may be efficient in the economist's sense of saving more income than it uses. Still the action may not be undertaken because it is politically unpopular, because it causes a pest-control condition which is esthetically unacceptable, or because it occasions a side effect — like the destruction of some wildlife on the endangered species list — which is ethically abhorrent.

In another context (Marty 1976) I have suggested that economic efficiency is only one of as many as seven tests that may be applied to a proposed action before it is judged acceptable. Acceptable control actions need to be economically efficient, of course. They also must be congruent with policies established by the organization undertaking the action; they must cause no substantially adverse environmental effects; they must cause no significantly detrimental economic, health or other impact to humans; they must provide an equitable distribution of benefits and costs; they must have an acceptable level of risk with regard to catastrophic outcomes; and they must be within the funding and organizational capabilities of the initiating agency.

Most decision-making turns out to be of this nature. We judge a proposed action to be acceptable if it meets a number of tests, and only some of these tests are economic. The economist can tell us whether economic benefits are likely to be larger than economic costs. He can also estimate who is going to receive those increases and decreases in income. So the economist can't tell us when an insect management action is acceptable, but he can tell us when it is unacceptable from the economic point of view.

There is a difference between economists and the biological specialists which has given some trouble in the past and, no doubt, will continue to do so. The biologist, whether he is an entomologist, a forester, an agronomist or what, tends to be most interested in the biological relationships among the insect pest, its host vegetation, its parasites and predators, and other components of the non-human biosphere. The social scientist, whether an economist, sociologist or what, is interested primarily in how these biological processes influence people. There is an obvious symbiotic relationship, but there is also a good deal of misunderstanding. I think I can highlight this difference in viewpoint best by comparing what biologists call insect impacts with what social scientists call insect impacts.

A good deal of the biological literature is descriptive of insect life cycles, of host preferences and the nature of host injury. A somewhat more interesting component of this literature deals with the mechanisms which bind the insect to its host, and govern the reactions of each to the other. From these studies come whatever ability we have to predict the course of insect infestations, and the timing and extent of changes in host plants that result. We know that host trees change in appearance, in vigor, in growth rates, in merchantable volume, and in susceptibility to injury by other vectors. We know also that there may be perceptible changes in other components of the biome as well.

But what is the significance of these changes to human beings? Let's consider a reduction in the merchantable volume of timber resulting from insect infestation. One recent report (USDA, Forest Service 1976) indicated that, for 13 National Forests in the Forest Service's Northern Region, the volume of timber destroyed by insects and diseases exceeded the volume harvested — an amount of timber sufficient, it was said, to construct more than 81,000 average-sized homes! The question is, would 81,000 more homes have been constructed if this pest loss had been prevented? Almost certainly not. Indeed it is difficult to see that any more homes, or anything else, would have resulted. These National Forests contain about 42 billion cubic feet of softwood growing stock, growth is

about 540 million cubic feet per year and removals are running at about 400 million cubic feet. Even with heavy pest losses, growth exceeds the harvest, and there is the equivalent of 100 years' supply of timber in the inventory. The economist would tell us that, although there may be a large physical loss, almost surely there is no economic loss. Little or no additional production of houses or other wood based products would occur if we caused growth and inventories to increase by undertaking pest control actions. Timber supply is simply not the limiting factor.

I hope this brief example serves to illustrate the difference in point of view between economists and biologists. Economists know that a biological change does not always mean a change in economic well being. Biologists need to bear this in mind too. Let me hasten to add that the reverse also may be true: that seemingly insignificant changes in biological conditions can have profound economic impacts. The point is this: the significance of biological change for economic well being depends on how that change influences the production and consumption of goods and services. Large changes sometimes yield little result, and vice-versa. Some changes have their human impact close at hand, while others cause an impact far removed in time or space. It is the economist's job to trace those impacts.

I've tried to make just two points here. First, that the economist can contribute to better forest insect management by translating impacts on trees to impacts on people. My second point is that the economist is equipped to deal with only one of the several kinds of impacts on people that forest insects cause — the impacts on economic wealth or well being.

Let me move on now to a review of the basic economic concepts used in evaluating the extent of impact and the desirability of insect management actions. I will be speaking in terms of an insect population control action on ownerships devoted primarily to timber production.

From the point of view of a private timber grower, the management of a destructive insect becomes interesting when the insect is, or will, cause a perceptible reduction in the value of his stumpage. And when there also is at least a reasonably effective means of reducing its level of injury. He then compares estimates of the cost of control with the value to be saved by control, to determine whether control is to his benefit from an economic point of view.

In some circumstances the control action can be applied at various intensities or levels. More intensive control means higher control costs and more value saved. He should choose the level of control intensity where the value of loss, plus the cost of control, is minimized. That is, he should continue to increase control intensity as long as the additional value saved is greater than the added cost of control.

While the costs of control must be met at the time the control action is undertaken, the resulting increase in timber values is not realized for several to many years in the future. Thus, the control action is like a financial investment, and is to be undertaken only if its return is larger than that which could be earned by using control funds for other investment purposes. This is taken into account by discounting the future income generated by control to the year in which the control action will take place, using a rate of compound interest which represents the best alternative use of funds. And it is this present value of future returns which is compared with control cost.

In some instances control results can be maintained or improved by undertaking a series of treatments during the period in the rotation when the trees are most susceptible to injury. And there may be interaction between the insect control actions and other management. For example, if there is considerable improvement in log quality as the result of insect control, then silvicultural treatments will be more beneficial with insect control than without it. Thus the grower may need to choose among a variety of total management programs, involving various frequencies of insect control, and various combinations of other treatments. These program alternatives can be displayed as a decision tree, which shows the timing of each potential action, its cost, and the value of stumpage at harvest for every possible combination of actions. A comparison of the present values of cost and return for each possible program allows the identification of the program which is best from an economic point of view.

There are, of course, many uncertainties in insect management. The response of the insect population to environmental factors and to control, the biological response of the host trees to various levels of injury, the cost of control and the value of timber saved — none of these are ever known with certainty at the time a control decision must be made. In situations when uncertainty is substantial the economic evaluation of alternatives can be repeated using different assumptions about uncertain factors. This process, called simulation by economists, can be useful in revealing the differences in uncertainty between alternate courses of action. If probability density functions are

available for uncertain factors their probability weighted expected values can be computed for the net present worth of alternate strategies using computer assisted Monte Carlo simulation.

The private timber grower tends to be concerned only about the economic costs and incomes which he pays or receives. But the economist does not take so narrow a view of the situation when a control action by a government agency is under consideration. Since the agency is acting on behalf of all citizens, the effect on everyone's wealth or income should be considered.

Many groups of persons are influenced by what forest owners and managers decide to do with their timberlands. First, there are those directly employed in forestry, logging, wood products manufacturing and shipping, and their families. Their continued employment and economic well-being are directly at stake. Owners of wood products firms have both profits and invested capital at risk. Adequate supplies of raw material can mean continued and even expanded production. Inadequate raw material supplies can mean business losses and eventual bankruptcy. Also impacted are those engaged in private economic activity of a secondary or service nature, where the volume of business and level of employment are significantly related to logging and wood products manufacturing. Then, too, there are the units of government — local, state and federal — that receive taxes arising in or related to the timber industries. Reductions in timber tax income impose an additional tax liability on all taxpayers in the affected jurisdictions, or result in reduced public service capabilities.

Recreationists and other visitors and users of forest lands also may be impacted. The nature, amount and location of pest control activities can significantly influence the type and quality of recreation available. All citizens may be influenced to one degree or another by changes in the quality of air, water, scenic, botanic and wildlife resources occasioned by timberland owners' and managers' pest control decision. Also, there are those who purchase and use wood products. The cost and availability of housing, paper products, furniture and a host of other common articles of every day life may shift perceptibly because of decisions about forest protection.

Economists can estimate the extent of these "stemming" benefits by input-output analyses of regional or the national economy. For example, Kaiser (1969) reported for the South in 1963, that a dollar of stumpage was processed into primary and secondary products worth more than 25 dollars, and created wage payments of six and one-half dollars. Economists are quick to point out that these stemming benefits cannot be claimed or counted as a benefit to additional timber utilization. This is so because, in the absence of the additional timber, similar final goods would have been produced from other raw materials. However, if there is substantial unemployment, and additional wood processing activity brings work to some who otherwise would not be employed, then at least some of the stemming benefits are a benefit of additional timber utilization.

The quantities of timber and primary wood products produced in any year, and their prices, are determined by a series of interacting markets. There are three groups of market participants: businesses and households all over the nation that purchase wood products, the industrial firms that manufacture these products, and the public and private forests that supply the necessary raw material.

Final consumers of wood products decide how much of these products they desire as a part of their total market basket of all goods and services. The result of these millions of individual choices is a fluctuating volume of orders for wood-based final goods conditioned by the size of the population, the general level of income, and how well wood products compare with substitutes with regard to their cost and utility. The businesses that supply this final demand make guesses about what their volume of business will be during the next production period, and place appropriate orders for primary wood products with firms supplying them. The expectations of primary wood products producers for sales, in turn, guides them in arranging for purchases of timber from timber producers. Thus there is an orderly sequence or chain of information from the final consumer to the timber producer with regard to the quantity of product needed.

These expectations usually are based on sales experience of the immediate past, tempered by consideration of anticipated seasonal and cyclical shifts known to exist in the trade. And normally they are based on the assumption that current prices will continue, or shift only marginally.

Prices change when the quantities of a goods offered are markedly more or less than the quantities wanted. Prices rise when buyers' wants outstrip sellers' offerings, because sellers can get a higher price under these circumstances. The bidding up of price in shortage markets accomplishes a necessary rationing of available supply. The price increase weeds out buyers who can't, or don't wish to pay the higher price.

A market, then distributes available goods among interested buyers through a price adjustment process. The going price at any particular time tends to be sufficiently high so as to eliminate buyers who cannot be accommodated with commodity supplies currently available. This same going price also acts as a signal to suppliers of the commodity. When prices advance sellers tend to increase offerings, if they can, to augment sales and profits. Falling prices tend to have the opposite effect on producers, causing them to restrict output or to abandon it altogether.

This price adjustment process has an interesting result when we consider increasing the level of timber production, say through the development and application of more effective insect management procedures. Prices for wood and wood products have been increasing more rapidly than other commodities for many years. There is little question that these increases will continue. Wood demand is expanding faster than wood supply, and this is quite likely to continue.

But when we are successful in increasing supplies we can slow down the rate of price increase and make things a little easier on consumers. McKillop (1974), for example, considered the price impact of intensified timber management on the National Forests and non-industrial, private timberlands. He estimated that by the year 2000 the program would add 3.6 billion board feet to annual output, an increase of about seven percent beyond what would have been produced without intensification. This increase in supply, he estimated, would cause prices to be about five percent lower than would otherwise be the case, and mean a savings in expenditures on softwood lumber of about 484 million dollars per year. Economists call this benefit a "consumers surplus."

The process used by economists to examine public projects, in insect management or any other activity, is called benefit-cost analysis. The analysis is structured so that the project under consideration, or several alternate projects, are compared with what will occur if no project is undertaken. Project costs, which are to be paid by the government agency undertaking the project, are estimated for each year during the life of the project. These are called direct costs, and are paid from tax revenues.

Two other categories of cost normally are considered: associated costs and induced costs. Both are paid by individuals or organizations outside the promulgating bureau. An associated cost is a cost which must be met by one who is a primary recipient of the project's benefit, in order to obtain that benefit. For example, if an insect management project increases recreation use in subsequent years, the additional recreationists served must pay the cost of travel, of subsistence and of the recreation equipment needed to participate in the recreation. The cost of the added recreation is the cost of the insect management project, paid by taxpayers, plus the cost of partaking in the recreation experience, paid by the individuals participating. An induced cost is a cost imposed on another family, business, or bureau as the result of the project. For example, a federal insect control project may require the cooperation of a state department of natural resources, who will contribute some of the necessary project cost.

On the benefits side, the primary benefit is the value of additional output stemming from the project. For some outputs, like timber or forage that are sold to users, the primary benefit is measured by sales revenue. For other outputs, like water, economic value must be measured at the point where it is utilized for an economic purpose. For example, additional water for irrigation is valued by estimating how much it will add to the incomes of the farmers who will utilize it. For still other outputs, like recreation or preservation of a preferred ecological condition, no attempt normally is made to assign an economic value.

Secondary benefits are those that result from the project in social units other than those who benefit directly. Secondary benefits exist in the stemming economic activity only when labor and capital are employed that would otherwise find no use. In large projects where the added output is enough to influence price a consumer's surplus benefit also is estimated. As with costs, benefits are estimated year by year for the life of the project. Some projects continue to have effects for many years. Frequently, benefit-cost analyses are made for an arbitrary period of time less than the true or actual life of the project, to facilitate the process of evaluation.

All economic costs and benefits are discounted to the beginning of the project using a rate of discount meant to represent the social rate of time preference. In cases where all important costs and benefits are economic, a straight forward comparison of discounted costs with discounted benefits will reveal whether the project has economic merit. If benefits exceed costs then the project is efficient in an economic sense, and is an appropriate use of funds.

The difference in the private and public point of view of the same project is instructive. The private grower considers only the costs he pays and the revenues he expects to receive. He does not

take external costs and benefits into account. Public decision-makers do attempt to include externalities. If external benefits outweigh external costs the project will appear more efficient to the public agency than to the private grower. This is the reason that governments must be the ones to undertake or subsidize projects that are economically efficient from an overall standpoint, but inefficient when only direct costs and benefits are considered.

When external costs exceed external benefits the project will look more efficient to the private grower than to the public agency. Such actions will be undertaken by private growers if direct benefits are larger than direct costs, even though costs are greater than benefits when externalities are considered. In these cases restriction and regulation of such private activity may be undertaken.

In some cases, for example in insect management on a wilderness area, no economic benefit may stem from the action. That is, no change in marketed products or services results. This does not mean that the action is without benefit, it is simply without economic benefit. In these circumstances, the analyst will calculate an average cost for the action. He sums up direct and induced costs, subtracts any secondary benefit, and divides the resulting net cost by, in this case, the number of acres protected. The analysis, thus reveals that protection of this wilderness area from catastrophic change will cost X number of dollars per acre. The decision-making must judge whether protection of the area is worth the indicated cost.

I have attempted here to review the major economic concepts that underlie evaluations of insect management actions. And I have tried to highlight the differences in point of view between evaluations made for private growers and those made for public agencies. Now let's look at the recent history of such evaluations.

I have made a not very careful search of the American and Canadian research literature, and for the ten years 1966 through 1975, I have found exactly eight articles and bulletins that deal in a substantial way with the economics of forest insect pests and their control. I excluded from my list the many articles and pamphlets that mention economic aspects only superficially, while dealing primarily with other facets of an insect problem. I suppose a more careful literature review might yield half again this number, although probably not more than that. It isn't very many studies, is it? To make matters worse, three of the eight were journal papers that dealt with their subject only in a generalized or theoretical way, something like my paper here today.

This is not the sum total of economic evaluations of forest insects. Some number of evaluations are made by various government agencies and private business firms each year, to support funding requests for major control actions and research projects. Unfortunately, except for analyses appearing in environmental impact statements, these evaluations seldom are published and almost always are considered administratively confidential.

Economic studies of forest insects typically have been of three types: studies designed to provide an improved theoretical basis for economic evaluation, studies which estimate the economic significance of insect injury, and studies that provide estimates of the economic costs and benefits of control. Rose's work (1974) dealing with spruce budworm on jack pine is an example of the development of an economic model specific to a particular insect and host plant. Much of the theoretical work of use in economic evaluations of forest insects has been done with reference to agricultural insect problems. The recent work by Feder and Regev (1975) is a case in point. Marshall's evaluation (1975) of the economic significance of spruce budworm in New Brunswick is an example of the second type of evaluation. Payne and others (1973) have given us a procedure for estimating the change in residential property value resulting from gypsy moth attack. This study falls in the third classification since it provides a part of the information needed to make control decisions.

There is now a major forest insect research and development program being carried forward by the U.S. Department of Agriculture. The gypsy moth, the Douglas-fir tussock moth and the southern pine beetle are the three forest insects under intensive investigation in this program. Judging by the research program for Douglas-fir tussock moth, with which I am somewhat familiar, the economic content of this program is only a modest part of the entire effort. Is this wrong? No, it is not. The first priority in this kind of research must go to developing and testing effective insect population control procedures. Until we can control insect populations we do not have any control capability, and so no pest management alternatives to choose among. The second priority, in my view, is to develop the ability to predict both the course of insect population dynamics, and the physical result of various population levels on tree growth and other forest characteristics of interest. Once we have an effective control technology, and the ability to predict accurately population and damage levels, then there will be a need for economic analysis procedures to guide control decisions. I fear that

economics will always get a back seat in research programs centering on specific insect pests. The entomological and mensurational aspects will always take first priority.

We certainly do need more research on the economics of forest insect management. Stark (1971) recently has written "... it has always been a matter of wonder to me (and lately slightly of suspicion) why forest economists have, in general ignored this problem." I think there really are two important reasons for this. First, an economist, who wants to contribute effectively to better forest insect management, has to spend a lot of time becoming familiar with a substantial body of entomological and mensurational research, before he can even begin his efforts. In my experience, this familiarization load is large enough to discourage many economists. This could be gotten around in large measure if we had more researchers with academic training both in entomology and in economics, but that's a rare combination.

The second reason why there is so little research in this area is that insect management programs do not bulk large in comparison with other aspects of forest management. Timber harvesting, silviculture, fire protection, road construction, recreation management and other activities typically account for a greater proportion of management time and funding than does insect management. Only the large scale, epidemic insect infestation draws much attention.

We have had far too much ad hoc economics in the forest pest management field. The typical experience has been for an economist to undertake an evaluation of a particular insect or disease problem, and then to go on to other sorts of economics research. This kind of research experience is too specific to be cumulative and productive in the long-run. And this kind of research is quickly out of date as well. New protection procedures, new forest management goals and values and new economic circumstances all too soon rob most economic evaluations of any current applicability. This pattern of research constitutes a very wasteful use of scarce economics research talent.

Instead of proceeding in this fashion I think it's time to try a different approach. I need to stress, at this point, that there really are two tasks to be accomplished. One is a research task and the other is one of application. On the research side we need a separate research program in pest management economics. I say pest management rather than insect management because the problems and control strategies for forest insects, diseases and animals too, really are interrelated, and we need to move toward a more integrated pest management process. Also, from the economist's point of view these problems take a similar technical form.

My economics of pest management research project would have the function of developing a basic and comprehensive model for evaluating the economic effectiveness of alternate detection and control strategies. The model should be general enough to be adapted to a wide range of important pest problems. The model should be capable of predicting all significant impacts on income and wealth which may stem from changes in forest conditions resulting from pest injury. These would relate not just to timber utilization, but to recreational and other uses, to the extent that they are judged to be significantly affected. This model would accept data on forest condition and utilization, period by period, and matching data on socio-economic conditions within the region of impact. And it would provide predictions of the cost and income flows that would be generated. Alternate prediction sub-models would be needed to provide a relatively crude predictor when relatively scanty input data were available, and more accurate and detailed predictions when more complete input data could be obtained. The business of providing prediction of how stand conditions change in response to pest injury, of course, would lie in other fields of research. Cross-project cooperation would be needed to insure appropriate interface.

A first generation model would require at least five years of project time and involve, probably, 25 scientist-years of effort. So this would be no small or inexpensive undertaking. At its conclusion, however, we would have the potential for a computerized process for projecting economic impacts of alternate pest management actions. A second five-year period would be needed to refine the model by evaluating its performance in application, and to develop a comprehensive set of economic data inputs for each major forest region and sub-region and each forest related economic sector. The model would then be ready to hand over to a service unit which would be responsible for providing standardized projections, on an as requested, short turn around time, basis.

So much for the research task. The second task is that of application. With back up projection capability of the sort described above, we will not need to assign professional economists to undertake evaluations of each contemplated control action. But we still will need someone in the pest management organization for this work. Let's call him or her a pest management analyst. The analyst is responsible for providing socio-economic impact projections for contemplated pest management

actions, and for auditing pest management actions once they have been instituted. The first half of the job, providing socio-economic impact projections, means that the analyst must develop the data required as input to the economic impact projection model, data which relates to his region and the particular pest management problem under consideration. He may also need to provide non-economic impact projections. His job is broader than just economics. If there is believed to be substantial health impacts, for example, which may be pest related, he would be responsible for obtaining estimates of this impact as well.

The second half of the analyst's job is to monitor or audit actual human impacts. The only way we can learn to better predict both the biological and social results of our pest management actions, is by observing the actual results of those actions. Thus, careful monitoring eventually will provide the basis for vastly improved predictive ability.

A research project such as I have outlined, coupled with analysts on pest management staffs, would constitute an effective melding of economics research and application. This is what is needed to get economics into pest management.

Let me say just three brief things in closing. First of all, I am convinced that forest pests, left unmanaged, sometimes can cause a good deal of unhappiness for many persons. Some of these persons are close to the affected areas and are well aware of the problem, while others, far removed, are affected in indirect and unexpected ways. Second, it seems prudent to me to undertake pest management actions only when the human benefits of such actions abundantly outweigh the human costs. Finally, I am convinced that economics and economists can assist in effective pest management decisions to a far greater extent than is the case today. But if that is to be we must work together to muster the necessary resources, create more positive working relationships, and carry forward the needed work.

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Section 12: Stored Products and Structural Insects

Tropical Stored-Product Entomology

Moderator: Peter F. Preveit (U.K.)

Tropical Stored-Product Entomology: Introduction

DR. PETER F. PREVETT

Ladies and Gentlemen:

It is, I think, a measure of the importance attached to tropical storage pest problems that this was the topic selected for the Congress Symposium in this Section of the Congress.

“Tropical Stored-Product Entomology” is not, of course, a subject in its own right. Much of the information which has been, or will be, presented to us in the Special Symposia of this Section of the Congress or which has been discussed within its Informal Conferences is of interest to those of us who have a special concern with stored-product pest problems in tropical countries. We have already heard contributions on insect control methods in use in different geographical areas, on stored-product insect ecology, on the use of controlled or inert atmospheres and other non-chemical methods, on infestation detection, sanitation and loss assessment and on host-resistance, and will, this afternoon, be discussing the all important subject of resistance to contact insecticides and fumigants.

The answers to our insect pest problems do not lie solely in the selection of suitable methods for insect control. It is essential not to lose sight of the importance of pre-storage factors in determining the susceptibility of a crop to pest infestation during storage. This will be to a large degree influenced by the extent of damage caused by harvesting and threshing methods and by the efficiency of drying, both in terms of adequate reduction in moisture content and damage caused during the drying process. Equally important are the basic characteristics of the grains themselves, as has been well demonstrated by recent work on the susceptibility of the new high yielding varieties of maize to infestation by *Sitophilus zeamais*.

It is true to say that in many tropical areas 70 percent or more of harvested production never moves from the farm into marketing channels. It is in this type of situation, with the small acreage farmer cultivating land often in close proximity to his store, that the problem of pre-harvest infestation of cereals and legumes by primary pests of storage is most acute, and we have contributions this morning which focus upon this and related problems. I would suggest that we already have a significant fund of knowledge and a range of possibly technological inputs which should allow us to have a considerable impact in this area. The need is primarily one of survey/identification, selection in relation to technical, climatic and socio-economic factors and implementation through communication.

When grain moves through the marketing chain into central storage, primary infestation is normally controlled by fumigation, following which the major problem in the case of grain stored in sacks in conventional warehouses is that of reinfestation by a different spectrum of pests, particularly *Ephestia cautella* and other moth species. Surface sprays rarely prove to be effective and there are often constraints to the use of space treatments or mechanical barriers. An alternative which may have potential and which we shall be discussing this morning is the use of synthetic sex pheromones.

The insecticides most commonly used in the tropics in recent years to protect grain are lindane, malathion and pyrethrins. In view of the disturbing revelations of the recent FAO “Global Survey of Pesticide Susceptibility of Stored Grain Pests”, more extensive sampling needs to be carried out to determine more precisely the patterns of resistance within countries and the extent of movement of resistant strains between countries through international trade channels. Although there are a number of promising alternatives to the use of malathion, which is the chemical in predominant use today, future programmes need to place more emphasis on prevention of infestation through improved storage conditions and better handling methods.

Much work has been done in recent years to evaluate physical methods for the control of pests, for example, airtight storage, which can be successfully applied in relation to all levels of storage, and the manipulation of the environment within a bulk grain structure through the use of aeration and we have a contribution this morning which describes work in this area. More attention needs to be given to the ecology of stored-product pests under actual field conditions, taking account of the variation in physical environment that occurs in different types of structure in different climatic zones. We need to give more thought to possible ways of modifying that environment in order to minimise pest development and reduce our reliance upon pesticidal chemicals. It is critical, therefore, for the entomologist and the engineer to work closely together.

Considerable attention is currently being focused, by national Governments and by multilateral and bilateral agencies, on the need for action to reduce post-harvest losses. However our first requirement is for basic surveys to be initiated to establish more precisely the nature and extent of these losses, using a standardised methodology, within and between countries, in order that meaningful and comparable data may be obtained. Such surveys need to be ongoing in order to provide a continuous evaluation of the effectiveness of, and justification for, storage improvement programmes.

In a number of tropical countries there has been established, normally within the framework of the Ministry of Agriculture or its equivalent, a unit with specific responsibility for the reduction of post-harvest losses in agricultural crops through survey, development, training and advisory/extension programmes. The development of such a focal point of storage expertise should, in my view, be given high priority by all Governments. The increasing importance, therefore, of training, in assisting us to meet our objectives cannot be over-emphasised.

I am sure, ladies and gentlemen, that our speakers this morning will lead us into an interesting and fruitful discussion.

Thank you.

Tropical Storage Entomology and the Small Farmer

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ABSTRACT

The physical, biological and technological characteristics of tropical storage are defined in relation to the scale of operations of the small farmer and his appreciation of entomological problems. The development and improvement of storage technology realistically based on local resources and competence are suggested as the major way of reducing the substantial losses in quantity and quality of stored tropical produce. Increasing research and development work in storage improvement is producing increasing awareness of entomological problems, and clear demonstration of the effectiveness of drying, disinfestation and storage hygiene are beginning to have major impact. The examples of development in Kenya, Zambia and Nigeria are discussed in the context of the future of storage technology in the tropics and the challenge of developing world food and population balance.

Although the storage of agricultural produce and the science and practice involved are many centuries old and have evolved over the years, the major characteristics of farming and the handling and storage of produce has not undergone a dramatic change in many of the developing countries of the tropics. The tropical farmer in general is considered a small farmer because of his low capital input into farming, the size of his farm, his dependence on personal labour and that of his immediate farm family, the low level technology input and the low level of total production. In a large number of cases, he is also a subsistence farmer producing, on his 1-2 hectare farm, enough to feed himself and his family and only a little extra for the market in order to provide the purchasing power for his limited additional personal and family requirements. In spite of this, the seasonal nature of production, with alternating wet and dry season, has always emphasized the need for storage facilities so that what is produced during the main growing season (wet season) can be stored for seed and for consumption for anything ranging from 4-6 months of the off-season. In some cases, the frequency of the occurrence of drought, crop failure, famine and other types of natural disasters leading to shortages of agricultural produce has necessitated the development and practice of methods for medium or long-term storage as is the case of the hermetic storage pits of the Borno State in north-eastern Nigeria and the eastern Provinces of Zambia. In addition, the requirements of modern processing industries has induced storage activities in order to provide regular supply of raw materials, although many such industries prefer not to rely on small farmer storage and supply and therefore establish and manage their own facilities.

In general, the development and improvement of the technology of storage of agricultural produce seem to be related to the nature of the production cycle and the duration of the period of scarcity. For example, there is greater consciousness of storage methods and practices in relation to a variety of grains and other produce in the seasonally-arid Guinea Savanna, Sudan-Savanna and Sahelian Zones of Nigeria than in the Rain Forest Zone, where the dry season is usually of 3-4 months duration. In this latter zone, there is usually not more than 5 months between one major crop and another, and there are many more food substitutes from the variety of roots, tubers and fruits which abound. Taylor (1974) commented that storage techniques, structures and methods in

the humid tropics are largely make-shift, whereas in the drier areas, they are highly evolved, diverse and often imaginative.

The traditional methods that have evolved from these practices have been described by Taylor (1974). Their major purpose is to reduce infestation of grain and prevent biodeterioration resulting in losses in weight and quality. They utilise mainly traditional and physical methods of disinfestation and control and have been modified to limited or great extents in an effort to achieve greater efficiency and prevent the staggering losses typical of tropical storage. In this paper, an attempt is made to focus attention on the adaptation and improvement of these methods as a basic infrastructure in improving tropical storage technology and the economy of agricultural production.

Tropical Storage

The true tropics lying between the tropics of Capricorn in the south and that of Cancer in the north and the subtropics, have well over 80 developing countries and 2500 million people and represents an area in which the average population growth rate of 2-3% per annum is among the fastest in the world. Unfortunately, these regions are characterised by:

- (i) an abundance of storage pests and spoilage organisms, both in types and numbers;
- (ii) extremely high prevailing temperature and, in some cases, humidity conditions (30-43°C for the hot dry areas and 21-35°C for the hot wet areas);
- (iii) the acceleration of the life processes of the major produce-deteriorating organisms (insects, mites and microorganisms) resulting in a higher magnitude of level of infestation and losses;
- (iv) difficulty and ineffectiveness of natural drying as a prelude to preservation;
- (v) the contrast between heating and cooling which constantly produces problems of condensation, moisture migration and spoilage.

Apart from these physical and biological handicaps, the socio-economic problems clearly documented by (Hall 1955), including lack of capital owing to the low-income of small farmers, poor prices for stored produce, poor organisation and policy, lack of education and to some extent resistance to change, further compound the problems. The recent trends of declining production of food and other agricultural produce, and the tendency for developing countries, in spite of their potential and resources, to import food from developed countries make tropical storage a priority area requiring specific well-planned and well-coordinated action in order to produce an impact capable of facing the challenge of preserving the entire production in the agricultural sector for human consumption and other forms of utilisation.

Tropical countries are even at present not obtaining the full effect of increased agricultural production where this is occurring, because between harvest and consumption by man or his domestic animals considerable quantities of food are destroyed by insects, rodents and microorganisms. Hall (1970) stated that in some tropical countries, losses during storage, processing and marketing may be as high as 50 percent. Wheatley (1973) pointed out that for maize, a major staple food in most tropical countries, direct and indirect farm losses varied from 23-35% leading to an overall annual loss of 2 M tonnes in developing Africa. Even F.A.O.'s conservative estimates of 10% annual loss in cereal storage in both farm and store would run into millions of tons for the major cereals such as maize, sorghum, millet and rice, and much more for the more vulnerable root crops in which storage techniques are rudimentary and rather unsatisfactory.

Advances have been made in the improvement of the methods of storage by the small farmer in the tropics, especially in the last decade. But this was not until after the sad experiences of the importation and adaptation of methods (e.g., aluminum silo storage) which did not fit the environment and the scale of operation of the small farmer. Experiences in Kenya and Nigeria, have shown that only about 20-25% of the cereals (maize in Kenya and maize, sorghum and millet in Nigeria) ever pass through the commercial marketing system. The bulk of the produce, sometimes not accurately assessed, is held by the small farmer and subject to his methods of storage and preservation. While it is important that the commercial produce should be adequately and effectively disinfested and stored (and this is already achieved admirably in some countries, including Kenya, Zambia and Nigeria), particular attention should be paid to the improvement of the methods adopted by the small farmer so that with the tools and methods within his technical and financial possibilities, he is able to derive more substance of greater quality from the produce that he stores.

Entomology and the Small Farmer

The small farmer in the tropics, in spite of what many might say, is conscious of the fact that the deterioration and losses that his produce suffers during the period of storage are due mainly to insects and rodents. While fungi and other biodeteriorating organisms are less familiar, the insects have been recognised as major enemies for centuries and methods ranging from hand picking to the use of admixture of various plant materials and extracts as insect poisons or repellants had been used. The biology of infestation is, of course, less well-known and the fact that apparently healthy and uninfested produce placed into a clean 'rhumbu' in one or two months often turned into a mass of insects, frass and damaged produce still makes the idea of produce 'generating life' not too far-fetched to the tropical farmer. Because of this and because of the ineffectiveness of the traditional methods of disinfestation, many farmers have learned to accept the inevitability of damage to stored agricultural produce, this attitude thereby generating the desire to dispense with produce as soon as possible after harvest. In the absence of alternatives, consumers have also learned to accept and use damaged produce at certain seasons of the year, and the irony of the pricing situation is that the further away from harvest the more expensive are the items of stored produce and the poorer the quality.

The experiences of pilot schemes in south-western Nigeria, described by Patel and Adesuyi (1975) and documented in the context of motivation and method by Taylor (1974) indicate that there is a fundamental need for education in the process of the introduction of improved methods of disinfestation and storage to local farmers. Where adequate attention is paid to education small farmers can be made to appreciate that infestations in many cases start in the field and adequate disinfestation measures should be employed even before there is visible evidence of insect activity and damage. Although farmers are not expected to imbibe details of the biology and cycle of infestation of stored products insects, simplified information along these lines given during farmers' short-term training courses at the University of Ibadan, Ibadan, in the context of the Badeku project referred to in Patel and Adesuyi (1975), has improved their appreciation of the problems and enabled them to explain on their own some of the interesting observations in produce disinfestation and reinfestation. In some cases, farmers now recognise the important insects such as *Sitophilus zeamais* and *Tribolium castaneum* as the principal agents of damage in maize in the humid tropics and sometimes can explain their relationships in the progress of infestation and damage.

The role of microorganisms is more difficult to appreciate although the need for drying is fully grasped and the effects of inadequate or no drying can easily be demonstrated. The designs of many of the storage structures in the wetter areas have largely taken this into account, although effective drying is often not achieved because of lack of precision in the dimension in relation to the requirements for drying and the rate of drying. The work of the African Rural Storage Centre, at I.I.T.A. in Nigeria, in the design and modification of the 60 cm wide crib for the humid lowland maize-producing areas is a major contribution in this area. The effective drying, rodent protection and disinfestation possibilities offered by this relatively simple and inexpensive method has become a major contribution to small farmer grain storage in Nigeria and many other countries of tropical Africa. It is being proposed that these methods be widely disseminated in form of package designs, by training and by extension education back-up.

In the storage entomology of the small farmer an important factor that must not be overlooked is storage hygiene. Often times, the results of improved methods are negated by lack of hygiene and the effects of endemic populations of insects and other organisms in the storage structures and area. Store hygiene must, therefore, be an integral part of the education and training of the small farmer. It should be pointed out to him that it is only when good and adequate drying, disinfestation and storage practices are combined with impeccable storage hygiene that satisfactory results can be achieved.

Future of Storage Technology

Although at present the bulk of agricultural produce resulting from the activities of small-scale farmers in the tropics are retained on the farm and stored and managed for domestic consumption, the developments in agricultural expansion and improvement are likely to increase these volumes substantially in the next few decades. In particular, the introduction of new, improved and

high-yielding cultivars of major grains and root-crops, the increased use of fertilizers and agro-chemicals and the improved management of crops are likely to produce sudden demands for improved storage technology in handling, disinfestation, storage and distribution. These developments are being anticipated in many developing countries of tropical Africa and steps are being taken to combine the improvement of traditional methods with facilities for large-scale handling disinfestation and storage for both short-term and long-term requirements. These developments must recognise the facts that inputs of improved storage structures, chemicals for disinfestation, and suitable containers for handling and distribution are the most important limiting factors. These factors combined with adequate storage education and technical advice must be made readily available to the small scale farmer within easily accessible distances.

The examples of Zambia and Kenya, and the proposals which are currently being implemented in Nigeria,¹ should serve to promote similar schemes in other parts of the tropics. In Kenya there is a combination of the improvement of drying and disinfestation methods at the farmers' level and a highly organised system of collection, rapid transportation to depots, disinfestation supervision and management that guarantee the reduction of losses to the absolute minimum and a high quality grain for consumption and limited export (Taylor and Adesuyi 1975). Chemicals such as lindane and malathion are made widely available to local farmers and improved methods of drying and holding ensure that even before the produce is delivered to the depots the quality is safeguarded. A similar scheme operates in Zambia where increasing quantities of maize handled and stored by the National Agricultural Marketing Board come from outlying small scale farmers. A large number of rural depots are established so that small scale farmers can bring their produce to the nearest depots as quickly as possible. The depots also serve to distribute inputs such as fertilizers, pesticides, jute bags etc. Disinfestation may be carried out at the rural depot or after evacuation to the major depots where stacks are fumigated with methyl bromide and the sacks are treated externally with fenitrothion. Hindmarsh and MacDonald (1975) have compared the efficiency of fenitrothion and pirimiphos-methyl as surface treatments for the control of insect pests of bagged maize and shown that fumigated stacks subsequently surface-treated with pirimiphos-methyl at the rate of 1.08 g/sq.m. protected the stacks from reinfestation by the main species for up to eight months. Apart from handling and transportation problems, this system could be efficient. It must, however, as it does, also take care of grain protection at the rural storage level. Admixture with malathion or lindane is still widely practised but the synthetic pyrethrins seem to show a lot of promise.

In Nigeria it is proposed that a number of rural state and Federal depots be established for the receipt, disinfestation and storage of grains. Considerable emphasis is placed on the improvement of the traditional storage structures so as to make them more efficient in drying, and amenable to the use of disinfesting chemicals and protectants. In humid southern Nigeria the improved crib is expected to form the basis of small farmer storage for four or five months, and fumigation in warehouse followed by stack treatment with residual insecticides are envisaged. A proposed network as originally conceived is shown in Fig. 1., and the relationships and rural depot proposals are indicated for part of the country (as example) are shown in Fig. 2. It is proposed that the agroservice-centres envisaged in the agricultural programme of the development plan should serve as rural depots to supply inputs for improved handling and storage, within easy access of small-scale farmers (Taylor 1975). These centres would serve a dual purpose of stimulating production by providing distribution services for improved seed, fertilisers, pesticides, technical advice and storage inputs such as instruction kits for crib building, or packaged materials for crib building; insecticides, jute bags etc. The recognition of the need to reach the small scale farmer for this purpose is a major departure from practice and an investment that is bound to yield substantial dividends.

It must not be forgotten that the tropical farmer has other storage problems especially with roots, tubers and pulses. The advances in the knowledge of disinfestation and adequate storage of roots and tubers are not as great as in grains and pulses. There is therefore the need to intensify efforts at improving the traditional methods so that losses due to respiration, moisture loss, sprouting, biodeterioration (fungi, nematodes etc.) can be reduced to the minimum. The extent to which success is achieved in relation to the problem of storage of grain, pulses, roots and tubers at the small-scale farmer level is likely to largely determine the success of handling the challenge of food, population and nutrition in the tropics for the rest of this century.

¹ Source: A Federal Grain Storage Scheme for Nigeria, Joint Consultancy Report of the Federal Grain Storage Consultative Group and the F.A.O. Security Mission 1976.

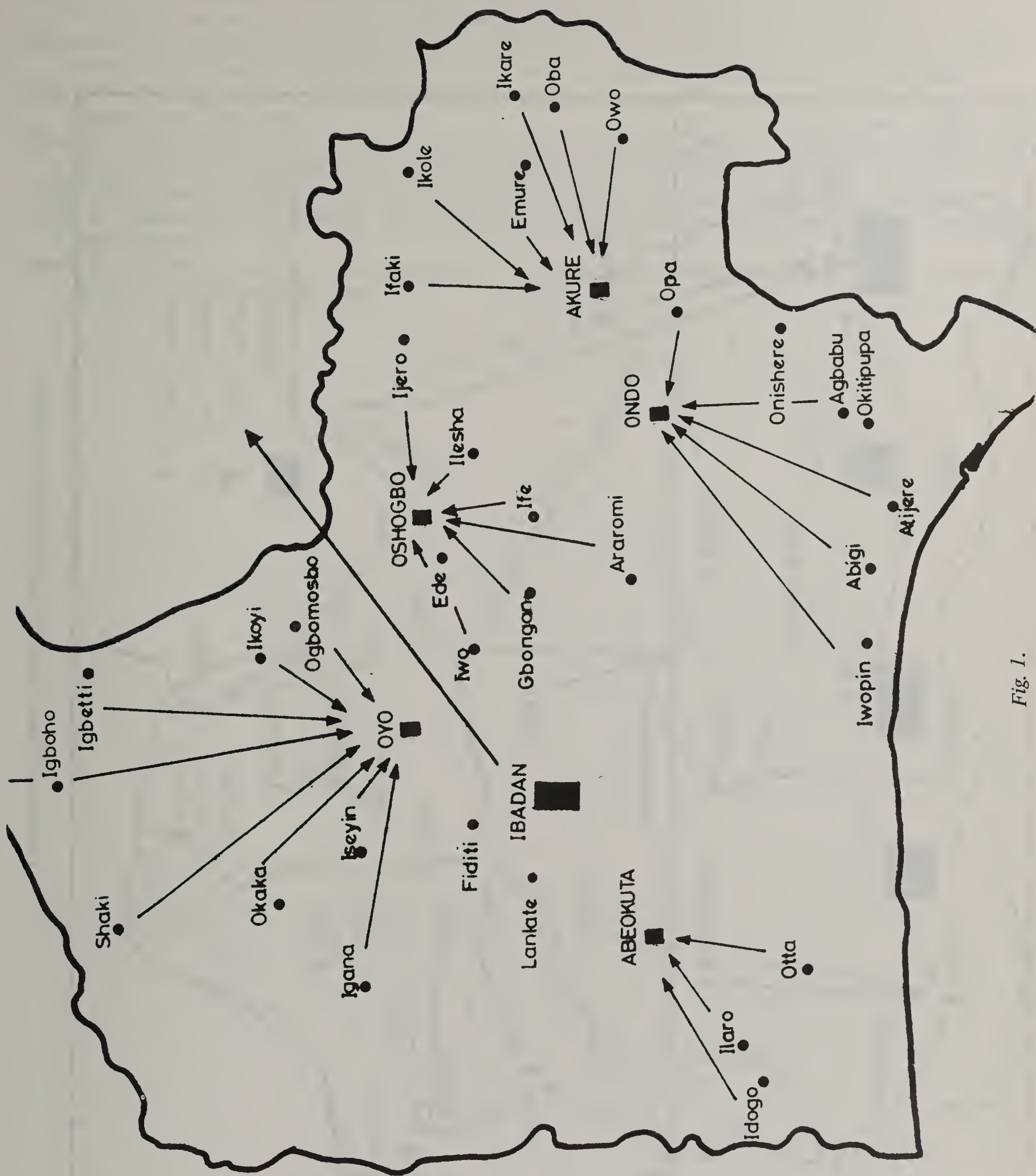


Fig. 1.

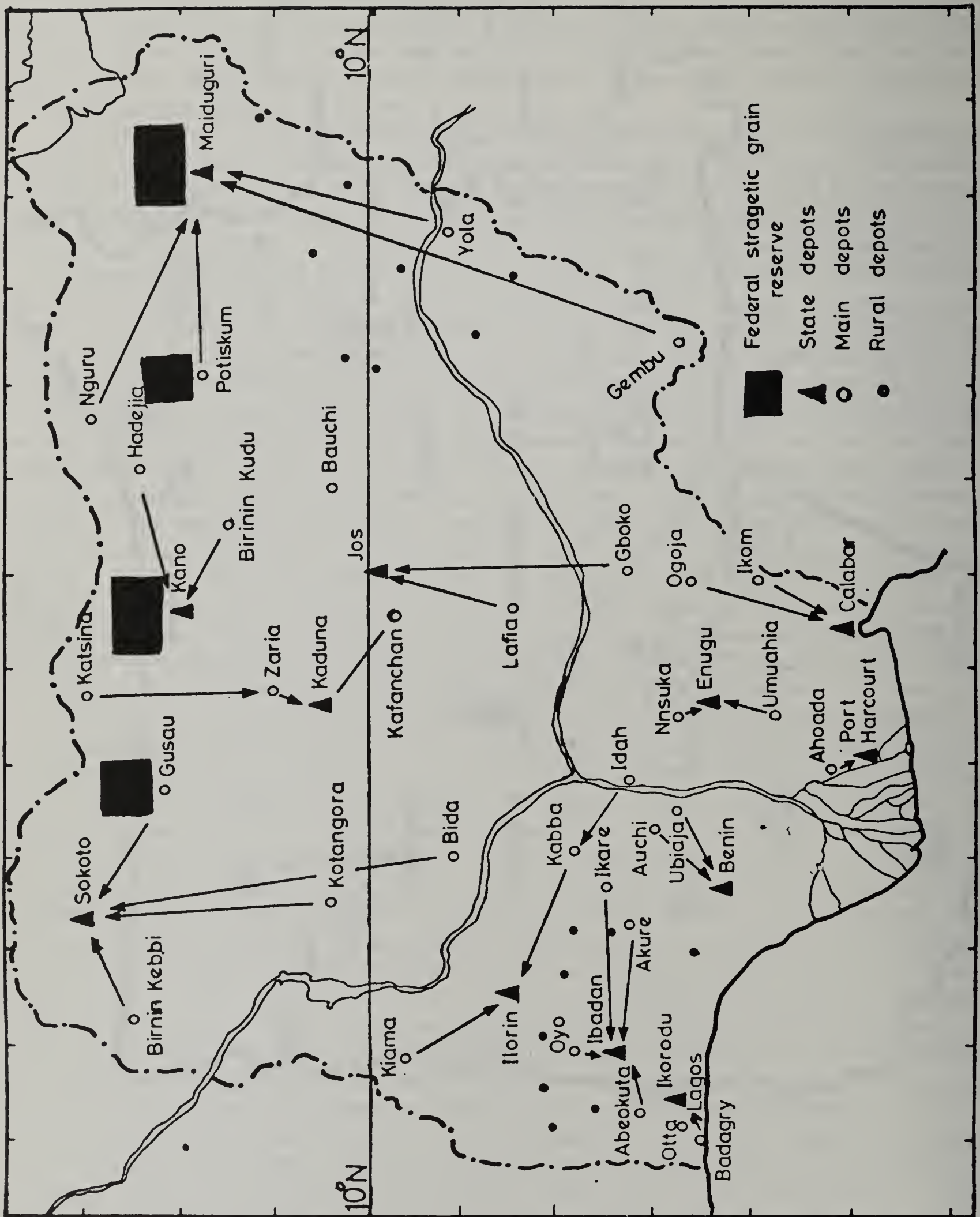


Fig. 2. — The siting of Federal and State grain reserves and depots.

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Distribution and Abundance of Insects in Butyl-Rubber/EPDM Silos Containing Wheat¹

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ABSTRACT

Observations were carried out over a 10-month period in a flexible silo containing 900 tons of wheat. The silo consisted of a butyl-rubber/EPDM welded liner inside a circular supporting weldmesh wall, and was designed to provide an airtight seal. Development of insect populations which became evident two months after the beginning of storage was arrested due to the airtightness, and gas concentrations unfavorable to further insect development were maintained.

Insect abundance was recorded in grain samples drawn from the upper layer of 30 containers during three storage seasons (1972-1975). The number of live insects per infested sample of grain reached 116 during October and was reduced to six in November. The insect population remained low until the end of the storage period. The insects found, in order of decreasing abundance, were *Cryptolestes* sp., *Oryzaephilus surinamensis* L., *Tribolium castaneum* (Herbst), *Rhyzopertha dominica* F., and *Sitophilus oryzae* L. Grain was preserved at a satisfactory quality throughout the storage seasons.

Storage of grain in flexible structures made of butyl-rubber is practiced in many parts of the world (Hyde 1974, O'Dowd 1971), as they have their distinct advantages. These silos can be transported and erected on any smooth ground and packed up and stored when not in use (Fig. 1). Because of the low permeability of the sheeting to atmospheric gases, the butyl-rubber silos enable application of the "airtight storage" method (Hyde 1974, Navarro et al. 1968). This method provides a useful means of insect control in dry grain without the use of toxic chemicals. However, certain problems arise in connection with the degree of airtightness which can be achieved. The butyl-rubber silos can be sealed to a satisfactory degree to control insects. However, different factors, including climatic conditions, have been reported to affect the butyl-rubber sheet, making the airtightness of short duration (Dedrick 1973, Hyde 1974).

Field tests on the distribution and abundance of insect species over extended periods in large structures having a satisfactory airtightness are scarce. The present work tested the airtight storage method in a butyl-rubber/EPDM silo and over three storage seasons the infestation levels in dependence on the use of other insect control methods in these structures.

Experimental Procedures

The tested flexible silos were of 1000-ton capacity and comprised three basic parts: a cylindrical bag with a conical roof fabricated of butyl-rubber (a copolymer of isobutylene and

¹ Contribution from the Agricultural Research Organization, Israel. 1976 Series, No. 210-E.



Fig. 1. —Butyl-rubber/EPDM silos at Qiryat Gat, Israel.

isoprene) and EPDM (a terpolymer) white laminate sheeting, a perimeter support wall, and a service aperture incorporating an inflation tube. Each silo had an overall diameter of 20.7 m and after filling it was approx. 6 m high at the apex. Grain samples were drawn through four sampling sleeves 7.5 cm in diameter, located on the roof of the silos (Fig. 2). A field at Qiryat Gat, Israel, was prepared on which to erect 30 such silos.

The observations on insect abundance and conditions prevailing in an airtight butyl-rubber/EPDM silo lasted 10 months, starting from June 1972. In these observations 900 tons of local wheat immediately after harvest, were conserved by the airtight storage method. The results on infestation levels and abundance of species recorded were based on data collected in a certain month of a year and refer to the pooled observations of three seasons (from June 1972 until June 1975). Each silo was loaded once during a storage season, which started in June of one year and ended in the following June.

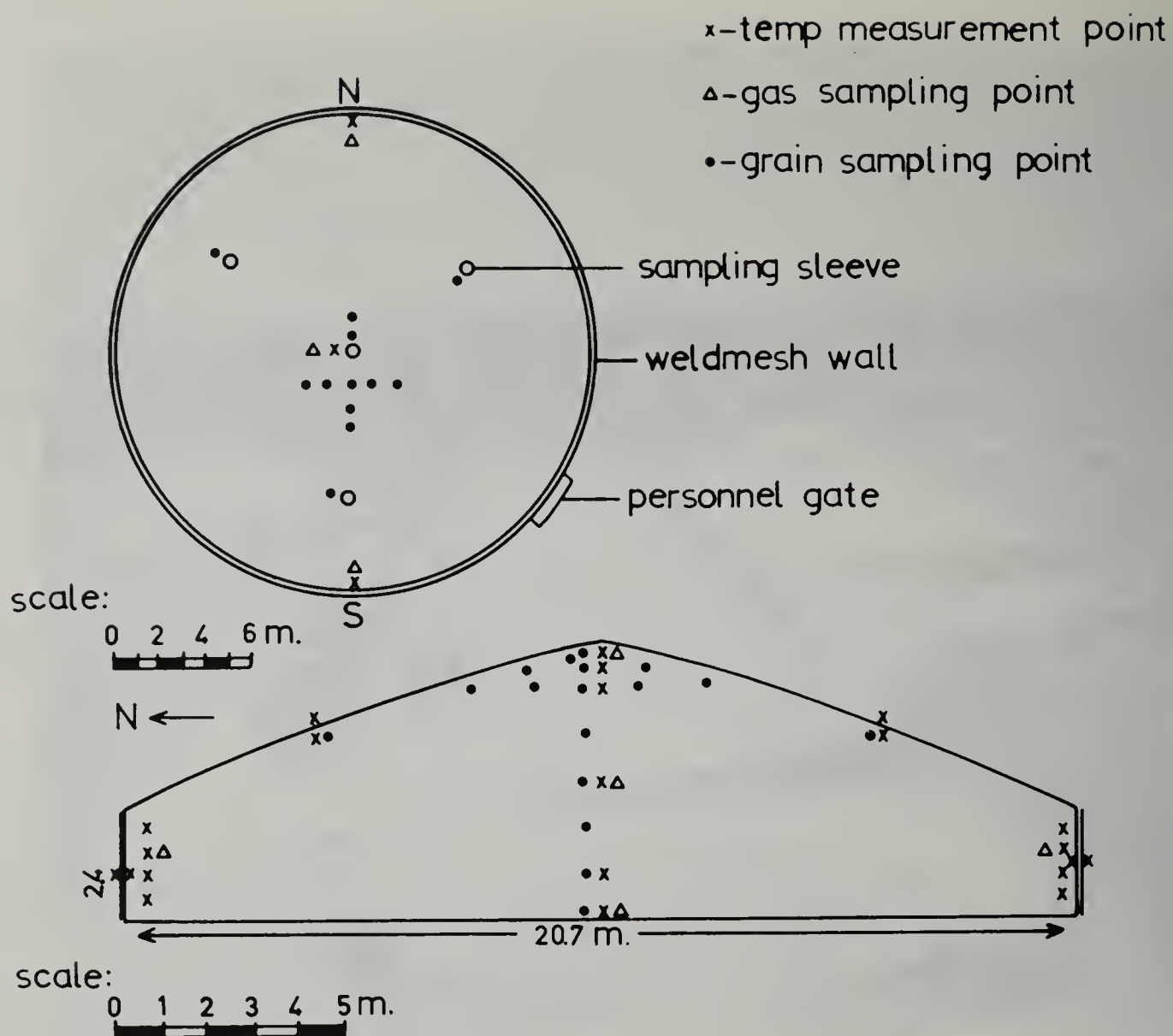


Fig. 2. -Temperature and gas measurement and grain sampling points in the butyl-rubber/EPDM silo in which the airtight storage was tested for 10 months.

Results and Discussion

Insect Abundance and Conditions Prevailing in an Airtight Butyl-rubber/EPDM Silo

Fig. 3 demonstrates the abundance of live insects found in grain samples (of 975 g) drawn from different depths at the center of a silo in relation to the changes in gas composition during the 10-month observation period. At the beginning of storage, no infestation could be detected and the slight decrease in oxygen tension may be attributed to some insect presence at locations distant from the sampling points. However, insect presence was noticeable in samples taken two months after the start of storage and this coincided with the decrease in oxygen concentration to 5%. In the subsequent storage period insects could not be detected in the low layers of the silo but were confined to an area 0-20 cm from the surface.

Oxygen and carbon dioxide concentrations, after reaching a certain level in October, started fluctuating in accordance with the changes in size of the insect populations in the silo. The dependence of the rate at which oxygen decreases, on insect population, temperature and degree of airtightness has been demonstrated by other workers (Hyde 1974, Oxley and Wickenden 1963). In these experiments, after a heavy infestation was eliminated, the oxygen concentration rose again. In practice it is very difficult to make a large container completely airtight. The fluctuations in gas concentrations shown in Fig. 3 were presumably due to the fact that the silo was not completely airtight.

The accumulation of insects at the apex of the silo and their disappearance from the lower layers of the bulk suggests that some migration may take place during storage. This accumulation of the insects at one point may be attributed to the interrelated effects of the following factors:

— The oxygen tension around the apex. The material of the sampling sleeves, located in the roof of the containers, deteriorated rapidly — permitting diffusion of oxygen from the outside. Although the oxygen tension in the sleeves was not measured, it was presumed that the cracks found

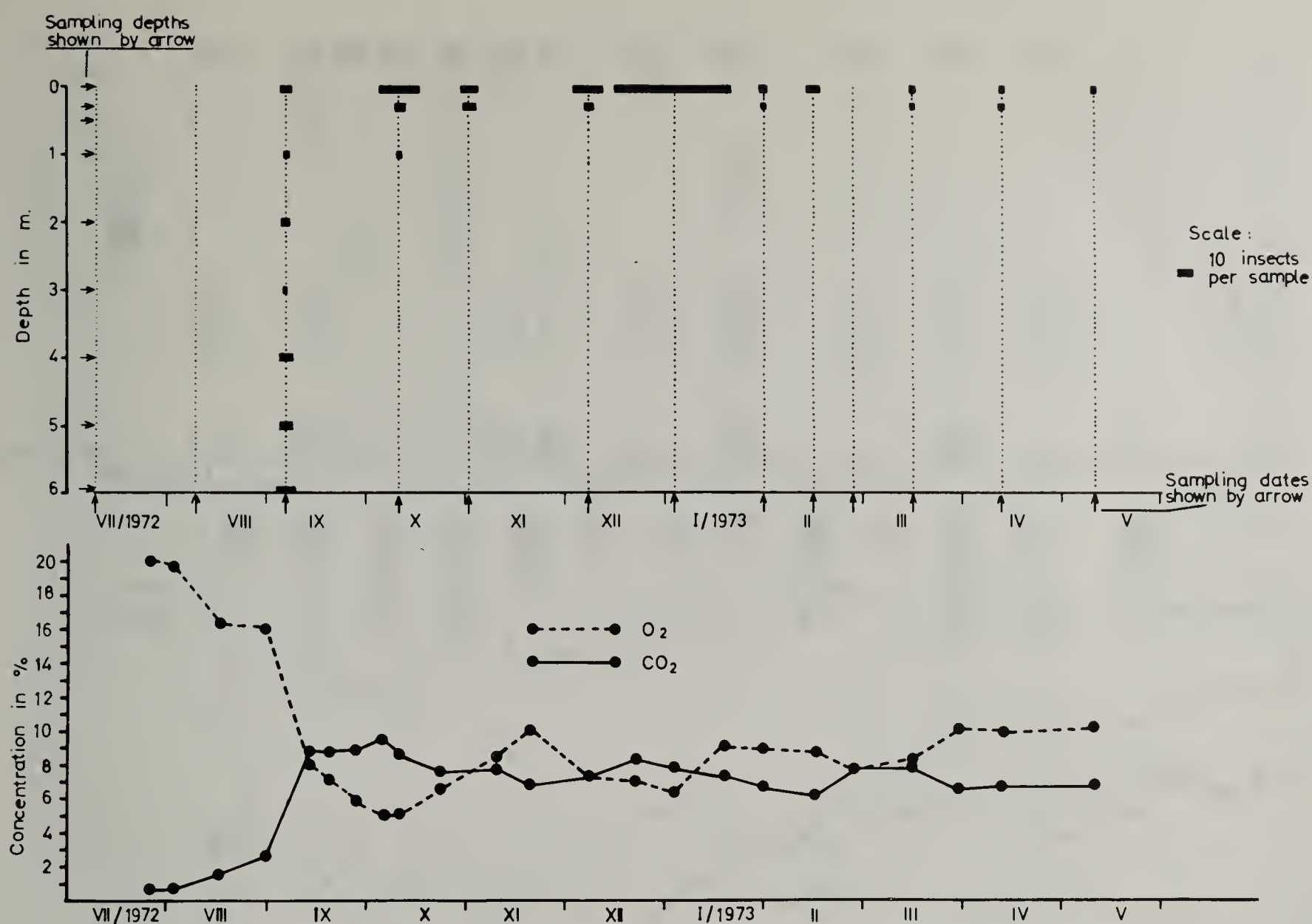


Fig. 3. —Distribution of live insects and change in gas concentrations in the butyl-rubber/EPDM silo, in which the airtight storage was tested for 10 months.

in the sleeve folds may provide a very confined space with a higher oxygen tension than at deeper parts of the silo, thus permitting insect survival. Opening the sleeves periodically for the withdrawal of samples obviously also permitted entry of air to the container, which produced, a high tension around the sleeves before it diffused into the container.

— Moisture accumulation at the apex of the bulk. In this type of storage the grain moisture content may increase as a result of translocation of water from the interior of the grain mass (Donahaye et al. 1973, Hyde 1974). Fig. 4 demonstrates the increase in moisture content at the apex of the silo during the storage period. It has been demonstrated that insects are attracted to wetter grain (Sinha and Wallace 1966), which provides a favorable environment for their reproduction compared with the low moisture content preserved in the deeper layers of the container.

— The temperature gradients prevailing at different layers of the bulk may also contribute to the accumulation of insects at the apex of the container. The high temperature of the grain, which was stored immediately after harvest, was found to dominate throughout the storage period (Fig. 4). Although the upper layer of the bulk was affected by the ambient conditions, the changes in temperature at the center and the bottom were less pronounced. During 10 months of storage the temperatures at the center varied between 33 and 40°C, which are less favorable for insect development than the temperatures at other layers (Fig. 4) (Howe 1965).

From the above data it may be concluded that the most favorable conditions for insect survival existed at the upper layer of the tested silo. The highest concentrations of insects were also detected at this region. These insect populations may derive from a static population being developed at the apex or from a mixture of insects migrating from other locations in the bulk. Additional tests in a similar silo gave the same tendency of insect accumulation at the apex. However, additional work is required to clarify this point.

Considering the grain quality preserved during the observation period, the airtightness level obtained in the butyl-rubber/EPDM silo could provide a satisfactory level of insect suppression and restrict grain damage.

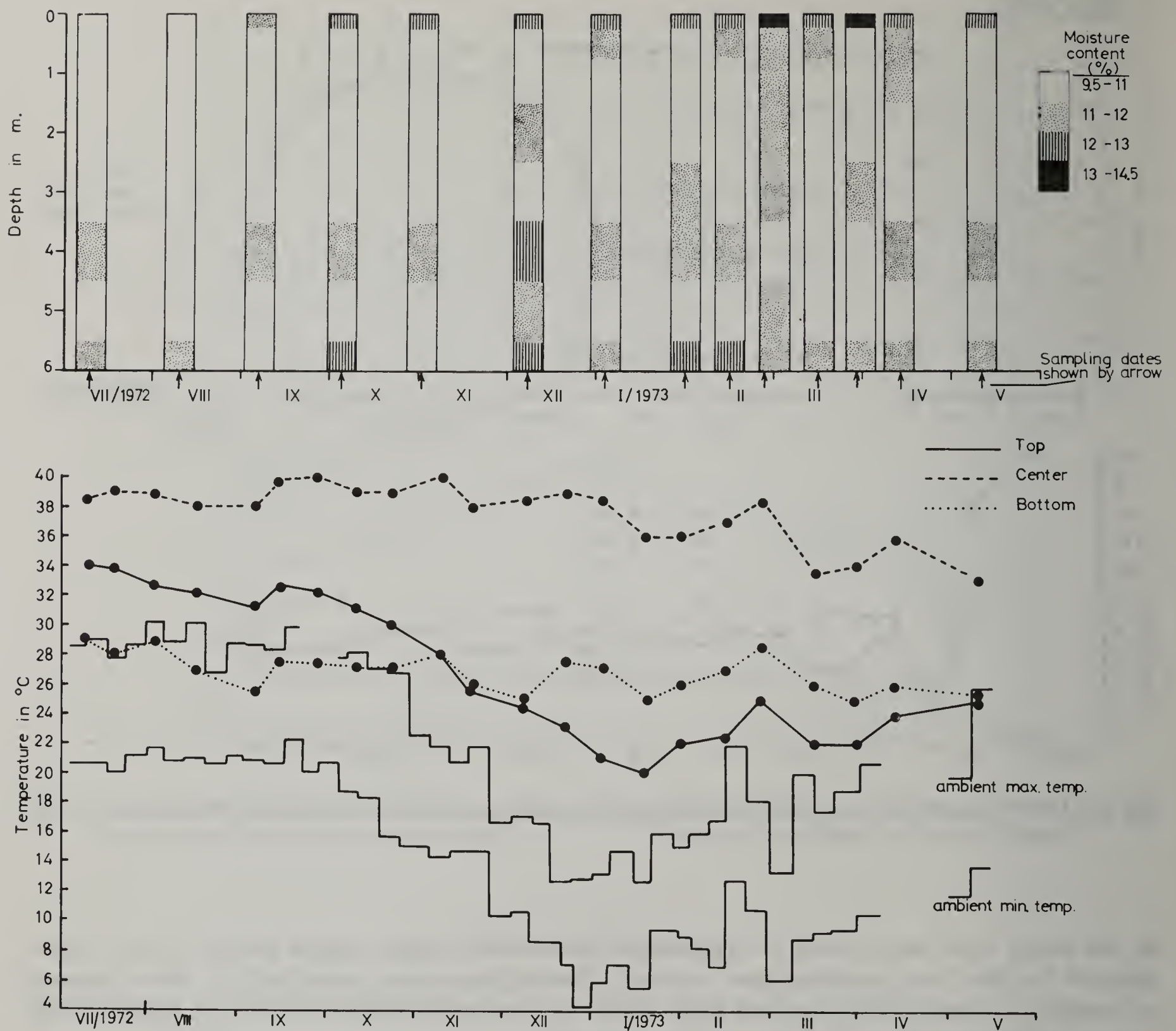


Fig. 4. —Moisture content, grain and ambient temperature changes during 10 months of airtight storage tests on the butyl-rubber/EPDM silo.

Infestation Levels and Abundance of Species Recorded in Wheat Stored in Butyl-rubber/EPDM Silos During Three Storage Seasons

According to the information obtained from the above and additional observations, the major insect presence was found in samples drawn from the upper layers of the bulk. Therefore, the following observations were carried out on grain samples drawn through four sampling sleeves in each silo, to a depth of 0-90 cm from the surface of the bulks. Fig. 5 shows the change in the mean number of live insects found in infested samples of grain (consisting of 715 g) throughout three storage seasons as determined in a certain month. Each storage season started in June immediately after harvest, and these results are a compilation from the samples drawn from the tested 30 containers. Accordingly, the mean number of insects per sample at the beginning of the storage period was low. The infestation level increased gradually following the storage, reaching a maximum of 116 insects per sample during October. The sharp drop in the number of insects to 6 per grain sample during November, can be attributed to the integrated control measures applied at greater intensity after September, as explained in the following.

In Fig. 5 the relative abundance of the insects found in samples taken from these silos is demonstrated. The dominant insect species during the first two months of storage was *Cryptolestes* sp. However, during August and later, the dominant species was *Oryzaephilus surinamensis* L., which

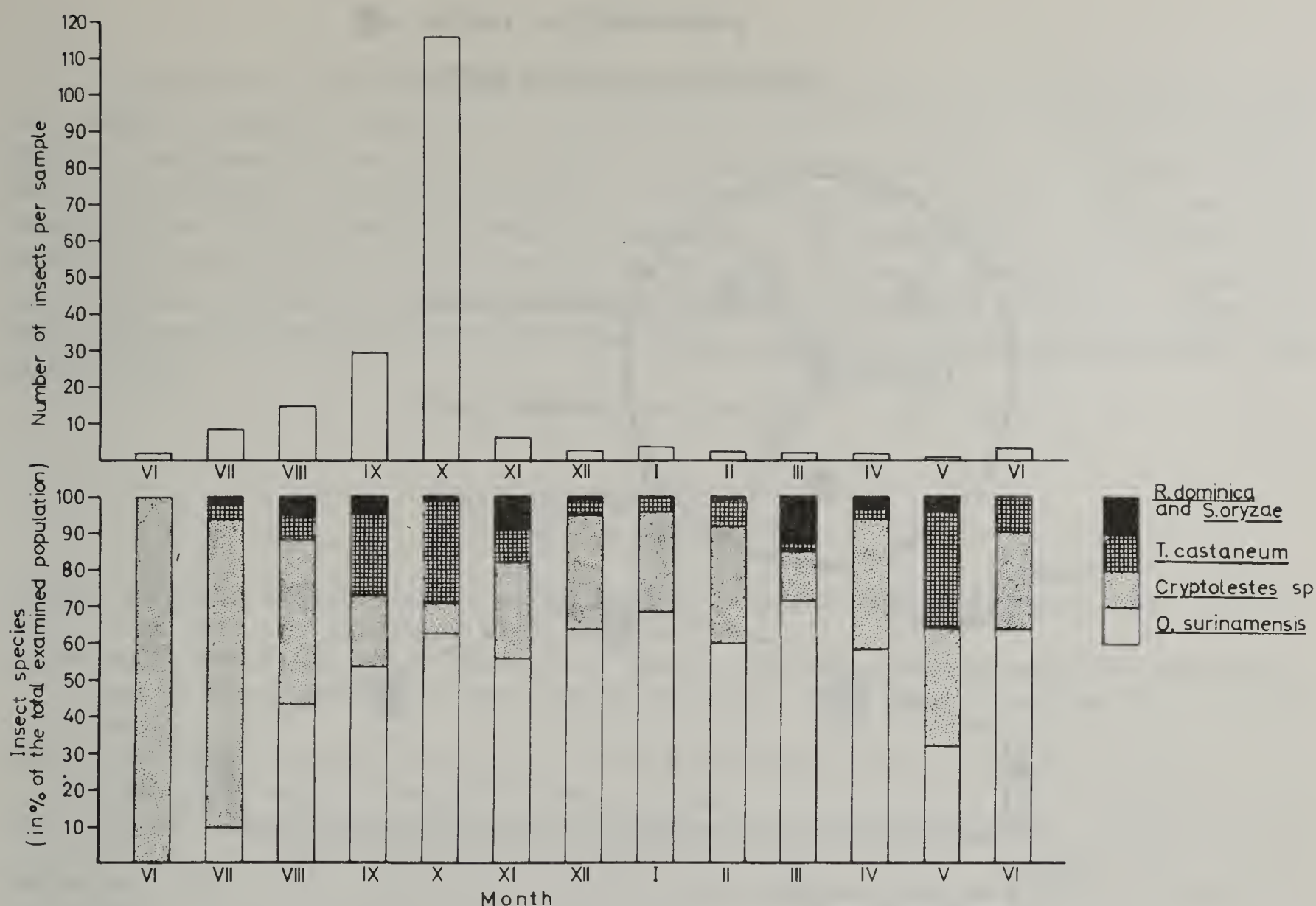


Fig. 5. —Mean number of live insects per infested sample and the relative abundance of different insect species according to storage month, as recorded throughout their storage seasons.

was recorded in high numbers throughout the storage seasons. *Tribolium castaneum* (Herbst) was also present, but appeared in greater abundance in September-October and May. Although *Rhyzopertha dominica* F. and *Sitophilus oryzae* L. were also present, they did not reach serious levels. This was due to the fact that their increase was prevented in all 30 containers by fumigation. This treatment was intended to control *R. dominica* and *S. oryzae*, being the most serious pests (LeCato 1975), and was carried out whenever they were detected in the samples.

The above tests and other experiments (6,7) indicate that these structures can be satisfactory in preventing insect damage of grain using the airtight storage method if there is no deterioration of the sheeting. However, extended tests showed that success in conserving wheat grain without notable loss was not possible in every silo. This was due to two main problems: moisture accumulation at the apex of the silos, and damage to the sheeting.

In most of the silos significant moisture accumulation was observed in the apex region, particularly at the start of the cold season and during it. To overcome this problem the containers were equipped with aeration systems (Fig. 6, Fig. 7). By using aeration it was intended to equalize the grain temperatures at different points in the bulks, to minimize the moisture migration, and to reduce the temperature of the grain — as a substitute for the airtight storage method of suppressing insect population development. However, the efficiency of aeration was, obviously, limited to the cold season (November to April).

Rodent activity, mechanical damage and deterioration of the butyl-rubber/EPDM sheeting, increasing with time, affected significantly the airtightness of the silos. In infested silos in which these factors prevented the production of an atmosphere with sufficiently low oxygen tension and the temperature was favorable for insect development, the grain was fumigated. Fumigation was generally effected with a dose of 750 g phosphine per 1000 ton of grain.

The conservation of grain in these silos (except the experimental silo during the first season) was thus possible by using three integrated means of insect control: airtight storage, cooling by aeration, and fumigation. The low level of infestation recorded during and after November, as shown in Fig. 5 demonstrates the effectiveness of these treatments, aeration and fumigation being applied more frequently, while the effectiveness of the airtight storage method was more limited with time.

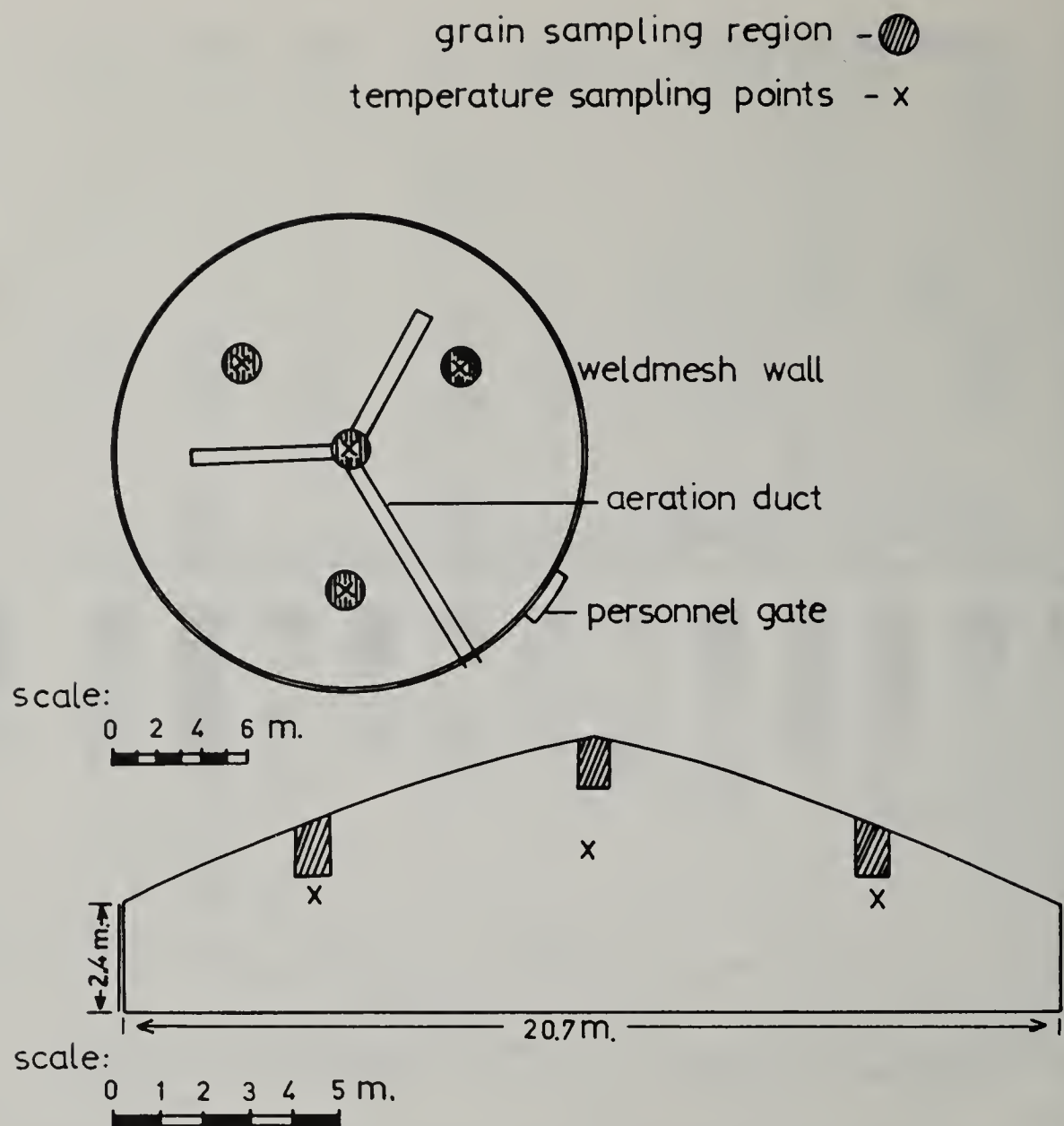


Fig. 6. -Plan of aeration system, temperature measurement points and grain sampling regions in the butyl-rubber/EPDM silos tested throughout three storage seasons.



Fig. 7. -Butyl-rubber/EPDM wilo. Aeration duct.

Conclusions

The use of butyl-rubber/EPDM silos is effective for conservation of grain at a satisfactory level using airtight storage as a means of insect control if the sheeting is not damaged. However, in practice, under the environmental conditions in which the observations were carried out, two main problems should be considered: moisture accumulation at the apex of the silos, and the damage caused to the sheeting. These factors provided favorable conditions for the accumulation of the major insect populations at the apex of the silos. The most harmful insect species, *R. dominica* and *S. oryzae*, and the other insect populations recorded, were suppressed. These silos continue to provide a satisfactory level of protection to the grain using control means such as aeration and fumigation in addition to the airtight storage.

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The Potential for Use of Synthetic Sex Pheromones for Control of *Ephestia Cautella* in Tropical Countries

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ABSTRACT

Synthetic sex pheromones can be used in a variety of ways in integrated pest management systems and offer particular potential in the confined environment of storage systems. However, applied research on pheromone use in storage systems has been minimal, especially in tropical storage situations. The author is investigating the use of such methods for control of tropical warehouse moth populations, and a summary of the results is presented. The future of pheromone control is discussed with emphasis on the need for practical trials in tropical situations.

Adult female insects often produce sex pheromones to initiate or control the mating behaviour of the males, and these pheromones can be identified and synthesized by the use of sophisticated techniques. The synthetic pheromones offer various possibilities for use in pest management, and these possibilities fall into three general categories. Firstly, the synthetic attractants can be used as a bait in traps to survey or monitor low-density populations of pests: this technique can be useful both as a field research tool and as an inspection technique for sampling low numbers of pests on high-value crops, especially where stringent quality control is enforced. Secondly, high-capacity traps or insecticide traps can be baited with synthetic attractants for mass-trapping of a pest population. Thirdly, the synthetic compounds can be released into the atmosphere to interfere with the normal pheromone communication and mating behaviour, thus decreasing the population growth of the pest. This last possibility can be theoretically achieved by three distinct techniques: (i) confusion of the males by permeating the atmosphere with synthetic attractants and thus disrupting the usual directional attraction of males to the natural female pheromone source, (ii) habituation of the males by permeating the atmosphere with one or more synthetic compounds to saturate the males' antennal receptor mechanism and (iii) inhibition of the males by releasing a repellent or inhibitory compound of the complex.

Applications in Storage Systems

Two basic characteristics of storage systems appear to offer advantages in the potential use of synthetic pheromones, namely: the relatively discrete populations of storage pests within the storage structure (when compared with the rather dispersed populations of pre-harvest pests), and the confined air space within a store (usually with minimal air disturbance). Because of these characteristics, one would expect that control of the pest population's fertility by synthetic pheromones would be unlikely to be negated by immigration (assuming that correct storage hygiene procedures are observed), and that it should be possible to maintain the necessary concentration of synthetic pheromones in the atmosphere by slow release of a small amount of pheromone material in the store. However, not all of the possibilities listed above are necessarily suited to all storage

situations. Thus, except for the control of low-density pests on high-value commodities, mass-trapping techniques are unlikely to be generally useful, since pest densities are often high and traps would quickly become saturated with the trapped insects. It is also thought that confusion and habituation techniques may not succeed for a number of reasons, e.g., the need to maintain a high concentration of synthetic pheromone in the store, and the possible danger of attracting male insects from neighbouring stores. Nevertheless, the potential for baited survey traps, for mass-trapping on high-value commodities, and for control by inhibition warrants investigation of these techniques, especially with respect to lepidopteran storage pests in central stores in the tropics.

Problems of Pheromone Research in the Tropics

In spite of the potential for use of pheromones in storage control, very little research has been conducted with the aim of producing practical control measures for storage pests, and the few studies undertaken have yielded disappointing results, e.g., Brady et al. (1975). Furthermore, no studies [apart from the author's current work on *Ephestia cautella* (Walker)] appear to have been undertaken in (or by) tropical countries. A major obstacle to applied pheromone research, especially in developing countries, is the correct identification and synthesis of all the components of a pheromone complex, which requires experienced specialists and costly, sophisticated equipment. However, various laboratories, mainly in developed countries, have concentrated in recent years on the identification and synthesis of such compounds, and many of the pheromones of the major lepidopteran storage pests are already known. It seems unlikely therefore that the lack of applied research is due to ignorance of the compounds involved.

Most of the biological work on pheromones of storage pests has been conducted in the laboratory from the viewpoint of behaviour and physiology of individual insects. Apart from the expertise and high costs involved in such research (which is thus not possible in many laboratories, especially in developing countries), knowledge of the behaviour of individuals cannot necessarily be extrapolated to an understanding of the ecology of natural populations (as noted in Brady and Daley 1975). Furthermore, the behaviour of an individual in an olfactometer (while it may yield results important to an understanding of the mechanism of pheromone reception) does not necessarily correspond with the behaviour of an individual in a natural population. It is therefore suggested that, if the objective is to investigate control possibilities, a more appropriate research strategy is to study the effect of the synthetic compounds in a natural population and only to resort to laboratory studies to examine specific problems encountered during field trials.

Research on Pheromones of *Ephestia cautella*

The sex pheromones of *Ephestia cautella* (Walker), a phycitid moth pest of many stored products in the tropics, are currently being studied at the Tropical Products Institute by the author and his colleagues, with the objective of developing techniques for control and survey of this pest. A summary of this research is presented below as an illustration of some of the suggestions made earlier in this paper, especially the ways by which field trials can be used to examine the feasibility of use of synthetic pheromones for pest management.

The identity of the pheromone components in *E. cautella* females were first confirmed, and the natural ratio of the components was analyzed, by Read and Beever (1976) who showed (by linked GC and EAG analysis) that the abdominal tip of a female contained three active components: (1) 5 ng of (Z) - 9 - tetradecen - 1 - yl acetate, (2) 10 ng of (Z,E) - 9,12 - tetradecadien - 1 - yl acetate, (3) 1 ng of (Z,E) - 9,12 - tetradecadien - 1 - ol. After synthesis, the basic functions of the three compounds (singly and in combination) were investigated by using traps, baited with the various test solutions, in cereal stores in Kenya (Read and Haines 1976, Read, unpublished data). These experiments clearly showed that compound 2 is the major attractant, that compound 1 has no attractive effect on its own but acts as a synergist to the major attractant, and that compound 3 strongly inhibits the attractive effect of compound 2 or of compounds 1 + 2.

The attractant combination has been used in slow-release vials as an attractant bait in sticky traps in the field. Tests are continuing, but it has already been shown that the baited traps were successful in sampling a very low-level infestation of *E. cautella* in a coffee warehouse where they could not be reliably sampled with unbaited traps. It is hoped that this method can be extended for mass-trapping of the moths on high-value commodities.

The inhibitory compound 3 has been studied for its potential use in control of mating in a natural population by slow release of a small dose of the pheromone from polythene vials in a Kenyan wheat store (Haines and Read, unpublished data). It was found that the usual proportion of virgin females (approximately 35% of all females) increased quickly to a level of about 70% which was maintained during the 4-week treatment. A similar increase was observed when the total combination of compound 1 + 2 + 3 was used, but in this case the proportion of virgins varied greatly on different dates, which was probably due to dependence of the confusion or habituation effect on the daily variations in store ventilation.

Recent trials to determine the effect of compound 3 on population growth have not been successful; it is thought that one or more of the unsolved problems (concerning the optimum dose of pheromone, the slow-release rate, the siting of the vials, and the maximum ventilation which can be tolerated) may be responsible for this failure. Such factors obviously need to be specifically studied in controlled laboratory conditions and small-scale field experiments before further large-scale trials are undertaken.

Discussion

The suggested strategy of field-testing of synthetic pheromones to investigate their control potential has some disadvantages. Firstly, such field-trials do not reveal the functional mechanisms involved in detection of, and reaction to, natural or synthetic pheromones, and such an omission is often dissatisfying to inquisitive scientists. However, it can be argued that much of the careful laboratory work on such functional mechanisms has also failed to produce helpful conclusions, and that those scientists directly involved in applied research can do much useful preliminary work on pheromones without a model to explain the precise functioning of these compounds. Nevertheless, refinement of applied techniques will eventually require such a model. Secondly, it is impossible to control the other factors present in a field situation, and field trials must therefore be carefully planned and, where possible, replicated or repeated.

The advantages of a field-experiment strategy are that the results of a trial can be easily translated into conclusions with direct applicability to the control situation and that, in the developing countries especially, such experiments can be easily conducted with a minimum of sophisticated equipment. These advantages have not been exploited fully in the past.

Apart from the possibilities for mass-trapping of low-density storage pests on high-value commodities, it is obvious that the use of synthetic pheromones for control must be viewed as part of an integrated control approach to pest management. Their potential in this area (e.g., in combination with fumigation under sheets to reduce population increase of *E. cautella*) seems worthy of more intensive research, and it is hoped that applied storage entomologists will use field trials to accelerate the previously slow progress towards a practical assessment of this potential.

Acknowledgment

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Pests of Stored Beans and Their Economic Importance in Latin America

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ABSTRACT

Although bean production in Latin America in 1968-71 amounted to 3.86 million tons per year, literature on bean storage and storage losses in this region is virtually non-existent. Among the most important storage pests are *Acanthoscelides obtectus* (Say) and *Zabrotes subfasciatus* (Boheman). The two species are similar but differ in oviposition behavior in that *A. obtectus* drops the egg among the seed, while *Z. subfasciatus* attaches them to the seed coat. *A. obtectus* is a pest in colder areas (higher altitudes or higher latitudes) infesting beans in the field and in storage, while *Z. subfasciatus* is confined to warmer areas and is a warehouse pest which does not attack beans in undamaged pods. Several minor pests reported in the literature to occur on stored beans may have accidentally been found on them.

In a survey of 30 warehouses in Columbia the average storage period for beans was 44 days. Although bruchids were considered the major storage problem, only 60% of the storeholders fumigated beans. In 20% of the warehouses beans showed the presence of storage insect attack. We hypothesize that due to the high susceptibility of beans to storage pests and the high value of the product, beans are stored for short periods. Under this system few losses from insect attack occur.

Dry beans (*Phaseolus vulgaris* L.) play an important role in the protein supply in Latin America. An average of 3.86 million tons per year were produced in the region during the 1968-71 period. This is about 34% of the world production of beans. About 60% of the beans in Latin America are produced in Brazil (Infante et al. 1974). With such a large quantity of beans produced in Latin America, which is the center of origin of beans, it is surprising how little documentation exists on the occurrence of and losses from bean storage pests.

The Insects on Stored Beans

The principal stored bean pests are two Bruchids, *Acanthoscelides obtectus* (Say) and *Zabrotes subfasciatus* (Boheman) (Table 1). Both pests are widely distributed being reported from Chile northward to the United States. While several other insects are reported on stored beans, they are of minor importance or only accidentally found on beans. They may have come from other stored products in the same storage area (Table 2). They have no economic importance on beans according to literature reports and our own observations, and in the following part of this paper only the first two mentioned species are considered.

Table 1.—The two principal pests of stored beans (Coleoptera, Bruchidae).

Acanthoscelides obtectus (Say)
Zabrotes subfasciatus (Boheman)

Table 2.—List of additional insects reported from stored beans.

Order, Family and species	Reported from	Reference
Coleoptera:		
Bruchidae		
<i>Acanthoscelides puellus</i> (Scharp)	El Salvador	Mancía and Cortez, 1975
<i>A. morosus</i> (Sharp)	El Salvador	Mancía and Cortez, 1975
<i>A. surrubresus</i> (Pic.)	El Salvador	Mancía and Cortez, 1975
<i>A. sp.</i>	El Salvador	Mancía and Cortez, 1975
<i>A. armitagei</i> (Pic.)	Brasil, Colombia	Ruppel and Idrobo, 1962
<i>A. chilensis</i> (Sch.)	Argentina, Uruguay	Ruppel and Idrobo, 1962
<i>A. obreptus</i> Brid.	S. and C. America	Ruppel and Idrobo, 1962
<i>A. obvelatus</i> Brid.	Mexico	Ruppel and Idrobo, 1962
<i>Bruchus rufimanus</i> Both.	Arg. Cuba, Pt. Rico, Perú, Uruguay	Ruppel and Idrobo, 1962
	Mexico	Peña and Sifuentes, 1972
<i>B. pisorum</i> (L.)	Mexico	Peña and Sifuentes, 1972
	Peru	Alata, 1973
<i>Callosobruchus analis</i> (Fabr.)	Brazil	Vieira et al., 1971
<i>C. maculatus</i> (F.)	N.S. and C. America	Mancía and Cortez, 1975
		Ruppel and Idrobo, 1962
<i>C. chinensis</i> (L.)	S. and C. America	Mancía and Cortez, 1975
		Ruppel and Idrobo, 1962
<i>Sennius bivulneratus</i> (Horn)	El Salvador	Mancía and Cortez, 1975
<i>S. discolor</i> (Sharp.)	El Salvador	Mancía and Cortez, 1975
<i>Zabrotes sp.</i>	Mexico	Ruppel and Idrobo, 1962
Anobiidae		
<i>Stegobium paniceum</i> (L.)	Chile	Ruppel and Idrobo, 1962
Anthribidae		
<i>Araecerus fasciculatus</i> (Degeer)	Brazil	Vieira et al., 1971
<i>Euparius sp.</i>	El Salvador	Mancía and Cortez, 1975
Bostrychidae		
<i>Rhyzopertha dominica</i> (F.)	Peru	Ruppel and Idrobo, 1962
Cucujidae		
<i>Cathartus quadricollis</i> Guerin	Brazil	Vieira et al., 1971
Curculionidae		
<i>Sitophilus granarius</i> (L.)	Chile	Ruppel and Idrobo, 1962
<i>S. oryzae</i> (L.)	Brazil	Vieira et al., 1971
	Peru	Alata, 1973
Dermestidae		
<i>Trogoderma simplex</i> Jagne.	El Salvador	Mancía and Cortez, 1975
Scarabacidae		
<i>Sericoides rufeola</i> (Sol.)	Chile	Ruppel and Idrobo, 1962
Tenebrionidae		
<i>Tribolium castaneum</i> (Abst.)	El Salvador	Mancía and Cortez, 1975
<i>Asida sp.</i>	El Salvador	Mancía and Cortez, 1975

Order, Family and species	Reported from	Reference
Lepidoptera		
Blastobasidae		
Blastobasis sp.	Chile	Ruppel and Idrobo, 1962
Galleridae		
Corcyra cephalonica (Stainton)	Brazil	Vieira et al., 1971
Gelechidae		
Sitotroga cerealella (Ol.)	Peru	Alata, 1973

Biology of the Principal Pests

The life history of the two principal bean pests, *A. obtectus* and *Z. subfasciatus* is broadly similar and is studied in detail by Howe and Currie (1964) who used an African strain of *Z. subfasciatus*. The principal difference is in their oviposition behavior. *A. obtectus* females scatter eggs among stored seeds, or when infesting beans in the field, they lay their eggs in cracks or cuts of the growing pods. The newly hatched larvae of *A. obtectus* wander freely, until they penetrate the seed. By contrast, *Z. subfasciatus* eggs are firmly attached to the seed. On hatching the young larvae bore through the eggshell and seedcoat in one process. The two species differ in their optimal condition for development. These are at 30°C and 70% R.H. for *A. obtectus* (in 27.4 days) and are for *Z. subfasciatus* at 32.5°C and 20% R.H. (25.0 days). Generally adults of *Z. subfasciatus* live shorter than those of *A. obtectus* (7.6 and 11.8 days, respectively) and lay less eggs (35.5 and 63.0 eggs per female, respectively) (Howe and Currie 1964).

Larvae of both species moult 4 times before pupating. During the last larval instar, the feeding and pupation cell becomes externally visible as a circular window in the seed as the larvae feed on the lower surface of the testa. After pupation the adult may remain in the cell for several days before pushing out the window. It has limited ability to escape by eating away the exit and here mortality occurs. Adults do not eat usually, but will take water or nectar. They lay their eggs rapidly after emergence and are usually short lived (Howe and Currie 1964).

Both species have a preoviposition period of less than one day, and eggs are laid at a maximum rate during the first days after emergence (Howe and Currie 1964).

Howe and Currie (1964) state that at 70% RH, optimal development occurs at 30°C, for *A. obtectus* and at 32.5°C for *Z. subfasciatus*. In our observations, *A. obtectus* is distributed over the higher latitudes and altitudes, while *Z. subfasciatus* is found predominantly in the warmer areas. Competition between the two species exists. In studies by Giles in Nicaragua (Giles pers. comm.) at 56 m, 45 m or 680 above sea level, beans were initially infested with *A. obtectus* (99.7%) and *Z. subfasciatus* (0.3%). After 16 weeks the ratios were 0:100% at 56 m, 4.6: 95.4% at 450 m and 27.3:

Table 3.—Life cycle of life of *A. obtectus* and *Z. subfasciatus* at 30°C and 70% RH. (Adapted from Howe and Currie 1964).

Development stage	Duration in days	
	<i>A. obtectus</i>	<i>Z. subfasciatus</i>
Egg	4.9	26.5
Larval and pupal	22.5	
Adult life (outside seed)	11.8	7.6
No. of eggs per female	63.0	35.5

72.7 at 680 m. The average temperatures at these three elevations were 28.2°C, 25.2°C and 24.3°C respectively. This indicates that *A. obtectus* is a stronger competitor at lower temperatures (Table 4). In the Cauca valley (24°C and 1,000 m) where CIAT is located *Z. subfasciatus* is the major pest of stored beans, and we have not found *A. obtectus* here. At CIAT *Z. subfasciatus* is a major post-harvest problem. We have not yet been able to establish colonies of *A. obtectus*, although our conditions are well within the range of environmental conditions for development stated by Howe and Currie.

Table 4.—Competition in storage between *A. obtectus* and *Z. subfasciatus* (from P.H. Giles, pers. comm.).

Altitude (m)	Avg. Temp. (°C)	Original rel. frequency <i>A. obtectus</i> : <i>Z. subfasciatus</i>	Rel. frequency after 16 weeks storage
56	28.2	99.7 : 0.3	0 : 100
450	25.2	99.7 : 0.3	4.6 : 95.4
680	24.3	99.7 : 0.3	27.3 : 72.7

Losses from Weevils

No precise information was found in the literature on economic losses in stored beans caused by insects. McGuire and Crandall (1967) estimate that for Mexico, Central America and Panamá storage losses are as high as 35%. They do not specify if these losses are from insects or other causes. *Z. subfasciatus*, was found in all countries surveyed, and *A. obtectus* was found in all these countries except El Salvador and Panamá.

In a marketing survey in Brazil (Recife area), 75% of the bean producers did not store beans. Average storage and handling losses, which are not specified, during the market process amounted to 13.3%. Those who stored beans used metal silos. (Slater et al. 1969).

Survey of Losses from Weevils in Colombia

To form a better idea about bean storage losses due to insects, we surveyed 30 Colombian warehouses, 18 in the Cali area and 12 in Medellin. Both cities are close to important bean production areas. Elevation at Cali is 1,000 m and at Medellin, 1,470 m.

Colombia principally produces red mottled beans, and only black beans when export markets are available. Beans are harvested in the various producing areas around June and December-January. Our survey was made in August-September 1975.

Farmers usually hand harvest and hand thresh their beans. The average length of storage on the farm ranged from 4 days (Departamento Nariño) to 38 days (dept. Huila). However, when black beans (planted in the survey period for export) were excluded, the on-farm storage periods were 2 and 8 days average, respectively (Economy dept., Bean Program, CIAT).

The average storage period in warehouses was 44 days, approximately the duration of one generation of stored grain insects at those altitudes. Of the stores surveyed, 63% held beans less than 1 week. Warehouse owners stated that bruchids were their principal problem in storing beans but only 60% of them stated that they had fumigated beans to control an insect infestation. Based on cleanliness of store rooms, construction, maintenance, organization of storage, etc., we classified 1/3rd of the warehouses acceptable for storing beans.

During the survey six of the 30 stores had bruchid infested beans. This means beans with adult bruchids, exit windows or perforations or eggs glued to the seed. The percentage infestation ranged from 0.2% of the bags present at the survey (among 600 bags) to 75% (among 12 bags). An average of

2.3% of all the bags surveyed were weevily. The percentage of infested seeds per bag ranged from 5-100%, averaging around 8%. It is therefore estimated that 0.2% of the individual beans were infested with weevils. All infested lots were, or were going to be fumigated.

Sixty percent of the warehouses refused to buy some beans in 1975 because they were weevil infested. The estimated refusal percentage was 5.1% of all beans offered. These beans were usually processed for animal feed. Therefore, the estimated losses of beans for human consumption during storage are estimated at 2.3% plus 5.1%, amounting to 7.4% (Table 5). Additional storage losses do occur from insect attack between wholesaler and consumer. Because of the high price of beans and the smallness of the retailer, which is mostly the public market place we estimate that this period is very short, and therefore will not greatly increase the losses due to insects. We observed that prior to the harvest periods beans are scarce and of poor quality. They are discolored, often shriveled, of mixed colors and this may explain why prices do not seem to be related to shortages. We are continuing our survey here, prior to and directly after the harvest periods.

Table 5.—Losses from storage insects in a survey of 30 warehouses in Colombia.

Percent of stores with infested beans	20.0%
Percent of bags infested	2.3%
Percent of refused bags due to weevils	5.1%
Estimated loss from weevils 2.3 + 5.1 = 7.4%	

All insects found attacking beans in this survey were *Z. subfasciatus*, except in one store where we found *A. obtectus*. We think that this does not represent the relative importance of the two species accurately, as during the period of our survey beans were shipped in from lower altitudes. At other times of the year the relative frequency of the two species of stored bean insects may be different.

Storing beans at the farm can be economically important due to price fluctuations. As an example, in the period from March-August 1974 the bean price increased by 65%, while from July-November 1975 the price dropped 21% (Table 6). The bean prices in each of the last 4 years declined from August to October and rose from October to August, and did not seem to be related to the harvest periods of June and December-January. Fumigation charges by commercial pest control operators were Col. \$5.00 per bag, or 0.24% of their market value (average 1975 prices). This cost doubles when the beans are picked up at the store, fumigated elsewhere and then returned.

Table 6.—Examples of changes in average bean price (Col. \$/Kg.) (Source DANE).

Date	Price	% change
March 1974	17.82	
August 1974	29.40	+ 65%
July 1975	35.34	
Nov. 1975	28.00	— 21%

Farmers and Non-chemical Control Measures

Local farm practice to control weevils is to apply wood ashes from fireplaces to the stored beans needed for future planting. The value of this method was tested by adding up to 20 g wood ash to 100 g samples of beans. As a physical barrier for the weevils, it appeared to be effective (Table 7).

Table 7.—Control of *Z. subfasciatus* with wood ash.

Ash addition (g)	% undamaged seeds, with ash applied	
	Before infest.	15 days after infest.
0	0	0.0
5	10.6	3.4
10	38.4	4.0
20	78.4	19.3

(100 g seed of Calima, infested with 10 pairs of adults for 3 months.

Storing beans in undamaged pods is a safe control measure against *Z. subfasciatus* attack. Eggs deposited on the podwalls hatched and larvae penetrated the podwalls but died inside the pods, without penetrating the seed (Table 8). The adults emerging from pods undamaged at storage appeared to have resulted from pods, which split open during storage and permitted adults to oviposit on the seeds in these pods (0.8 eggs and adults per replicate average). Although effective for *Z. subfasciatus*, this method cannot be used to control *A. obtectus* as this insect is able to attack beans in the pods. Labeyrie (1957) showed that storing beans unshelled or delaying the harvest greatly enhance *A. obtectus* attack. The practice of storing beans together with the debris from threshing, as compared with clearing away plant debris, soil, etc., had little effect on controlling *Z. subfasciatus*. Presence of 20% by weight of plant debris added to beans resulted in 88.4% undamaged beans after 3 months as compared with 99.8% in the samples without foreign material.

Table 8.—Development of *Zabrotes subfasciatus* on shelled and non-shelled beans.

Treatment	No. eggs/♀	No. adults/♀
Shelled	29.1	23.2
Undamaged pods	0.8	0.8
Damaged pods	23.1	16.0

Another farmer practice is being investigated. In Asia and Africa pulses are protected against Bruchid attack by vegetable oils. Another non chemical method for controlling weevils is the use of black pepper. One gram of ground pepper per 385 g beans reduced infestations of *A. obtectus* by 78% after 4 months storage compared with untreated lots. At 4.26 g per 385 g the reduction was 97.9% (Lathrop and Keirstead 1946).

Table 9.—Mortality of *Z. subfasciatus* adults 96 hours after infesting seed treated with malathion and lindane (after P. Golob, pers. comm.).

Product	ppm	% mortality when infested	
		Immediately after treatment	20 weeks after treatment
Malathion	8	85	0
	12	99	0
Lindane	2	100	85
	4	100	97

Inert dusts, especially crystalline silica, bentonite and magnesium carbonate were effective in killing *A. obtectus*, especially the fraction of the finest particles of a dust was most effective. The killing of adults (50% killed in 12 h, for bentonite) was ascribed to dessication (Chiu 1939).

In our laboratory we tested about 700 accessions of *P. vulgaris* for resistance to *Z. subfasciatus*. Several accessions rated very resistant, but some of these were classified susceptible when tested in the next generation. We cannot explain this change in resistance classification, but contribute it to environmental factors, and sampling error not too breakdown of resistance nor to weevil strain selection. Seed should maintain its resistance for at least 3 generations of testing before it can be called resistant and used for further studies. Resistance to *A. obtectus* has been reported by other authors (e.g., Lefebvre 1950).

Chemical Control Methods

Chemical control of weevils is readily obtained with a variety of products. Of the many references on chemical control only a few are cited. We assume that based on literature informations best suited for on-farm use are: malathion (P. Golob, pers comm.) and pyrethrins (Sales and Ruppel 1959, McFarlane 1970). These products were also effective under our experimental conditions.

In our survey most warehouses used only few products to control stored insects. A total of 33.3% of the warehouse owners used phostoxin, 40% used methyl bromide, 26.7% used CS₂, and 13% used pyrethrin. One store owner confessed he used aldrin to control bruchids. They stated that CS₂ had affected quality of the beans. It "burned" beans prolonging the required cooking time.

Future Research

There is a great lack of knowledge about the importance of bean storage and storage losses from insects. Surveys are needed to establish the importance of these losses. On-farm storage methods in particular should be investigated. Farmers can gain economically by storing beans to wait for better prices and storage should also help to stabilize prices as well, by providing a more continuous supply. Chemical as well as non-chemical insect control measures for properly designed storage units should be developed, as has been done in Africa by the Tropical Stored Product Centre.

The distribution of the principal stored product insects is not understood. Biological data from laboratory experiments do not explain why *A. obtectus* is found in the cooler regions, while *Zabrotes* is principally found in the hot climates. Also the competition between the two species is not understood when they are confined to storage areas. The competition appears to be related to ambient conditions.

Search for resistance to the principal stored grain insects should continue. This resistance may not affect the nutritive value of beans and should be incorporated in commercial varieties.

Acknowledgment

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An Ecological Study of Traditional On-farm Maize Storage in Kenya and the Effects of a Control Action

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ABSTRACT

Maize in Kenya is traditionally stored on the cob in basket-type stores. A study conducted in several areas in Kenya showed that climatic conditions play an important role in determining the rate of development of the two main pest species *Sitophilus zeamais* (Motschulsky) and *Sitotroga cerealella* (Oliver). The interactions between these two pests are found to be complex with *Sitophilus zeamais* gaining initial ascendancy and *Sitotroga cerealella* obtaining dominance later in the storage season.

An examination is made of the effects of parasitism. Parasitism of *Sitophilus zeamais* is noted to be negligible and parasitism of *Sitotroga cerealella* is shown to be of low significance in terms of population control.

The effects of retaining the sheath cover on maize cobs; of dusting unsheathed maize cobs with 2% malathion dust (at 10 parts per million); and of fumigating the unsheathed maize cob with phosphine gas (by use of phostoxin tablets) are examined. It was found that for storage periods of up to 3 months the fumigant treatment was the best means of control. For longer periods of storage the malathion dust treatment is superior.

Maize in Kenya is traditionally stored on the cob in basket-type stores. Specific storage methods however, differ from tribe to tribe and are influenced by socio-economic conditions. Generally however, the practice is to put maize on the cob without sheath covers into the store. The current control recommendation is the use of a 2% malathion dust at 10 parts per million.

Over the past few years the author has been involved in a detailed ecological study of the pest status of the two main storage pests in Kenya the maize weevil *Sitophilus zeamais* (Motschulsky) and *Sitotroga cerealella* (Oliver). Maize in Kenya is grown over a wide range of ecological and climatic conditions ranging from approximately sea level at the Coast to over 2000 metres in the highlands of the Rift Valley. Kenya's position on the equator has the effect of reducing the monthly temperature variation throughout the year to less than 5°C. Thus the average maximum and minimum temperatures are very closely correlated with altitude (Allan 1971).

The ecological study that the author conducted, was a series of experiments in 20 places in the country and involved following the rate of pest development by the extraction of samples at monthly intervals from an experimental bulk of 1000 maize cobs. Following the conclusion of these ecological investigations a study was made of control methods first in 12 and afterwards in 8 representative areas.

The work mentioned in this paper will provide in summary some of the effects of differences in ecology of grain storage in four areas and also the effects of a control action in the same areas. The detailed studies mentioned above will be described more fully elsewhere.

Development of *Sitophilus zeamais* and *Sitotroga cerealella* in the 4 study areas

The four study areas presented in this paper are from four different provinces in the country. There is Embu from the Eastern province, Kericho from the Rift Valley province, Bukura from the

Western province and Kisii from the Nyanza province. These four areas are fairly representative of the provinces from which they are drawn on most aspects of grain storage problems.

In all four areas it will be observed (Fig. 1) that *Sitophilus zeamais* are present in the grain at harvest. In only one place, in Kisii, we observe that immature stages of *Sitotroga cerealella* are also present at harvest.

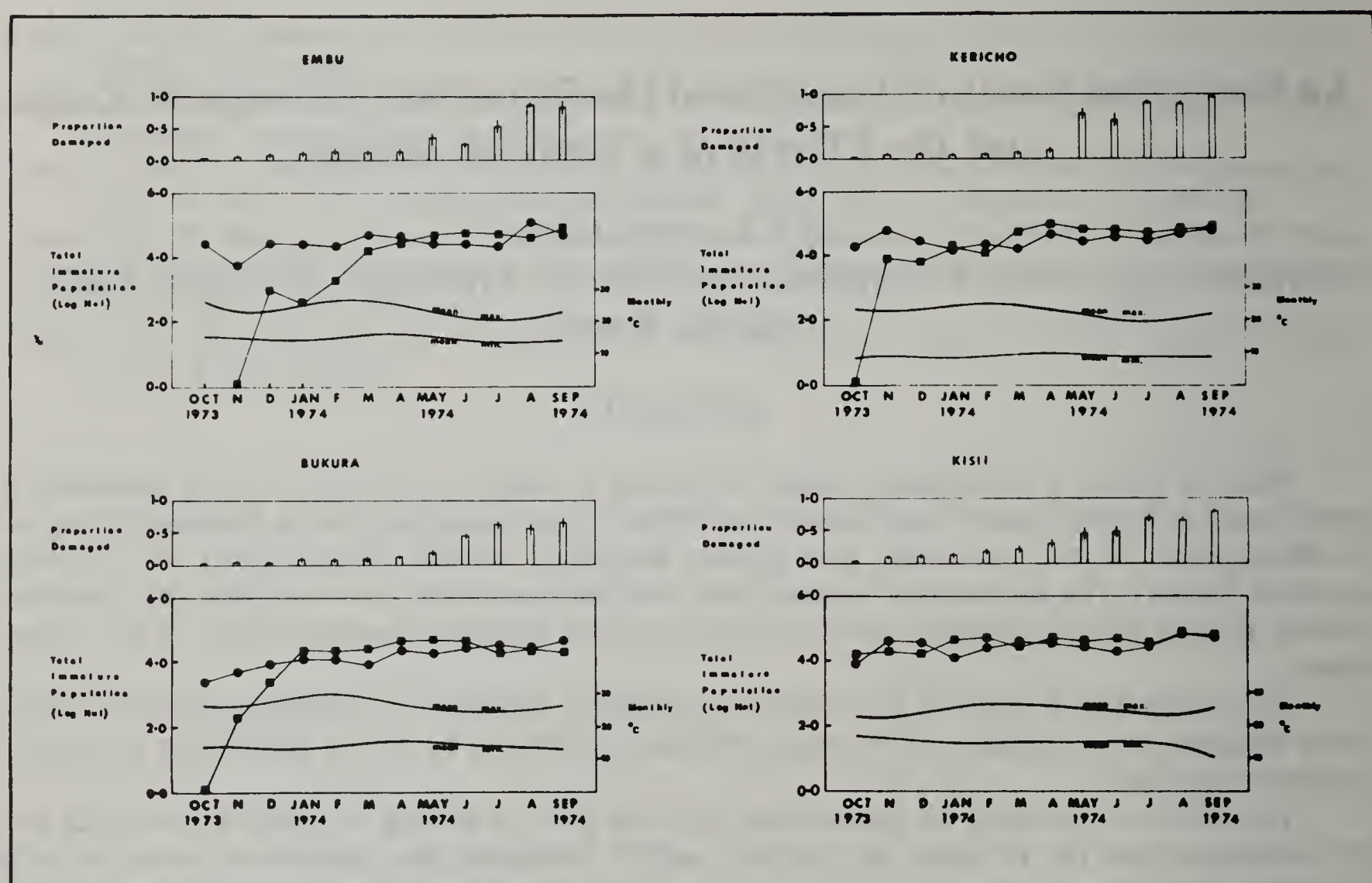


Fig. 1. —Monthly population census of immature *Sitophilus zeamais* (●) and *Sitotroga cerealella* (■) in four representative places in Kenya and a mapping of corresponding damage levels. Mean maximum and mean minimum monthly temperatures are also shown.

Sitophilus zeamais

Once established at harvest, the populations of this insect increase gradually in the initial month but thereafter maintain a steady oscillation between the 10-100 thousand range (Log. 4 to Log. 5). *Sitophilus zeamais* takes advantage of this early start to maintain dominance over *Sitotroga cerealella* in the first few months after harvest. However, as the graphs show, *Sitotroga cerealella* subsequently approaches and then maintains a slight edge over *Sitophilus zeamais* populations.

Sitotroga cerealella

In Kericho and Bukura immature *Sitotroga cerealella* appear in dissected samples in the first month after harvest and in Embu is recorded after the second month. As already mentioned it is present at harvest in Kisii. The initial rate of increase of *Sitotroga cerealella* is much slower than *Sitophilus zeamais* but subsequently it becomes dominant in terms of immatures present in the grain.

Temperature effects

The variation in temperatures from maximum not exceeding 25°C and minimum below 10°C in Kericho and maximum well over 25°C and minimum well above 10°C in Bukura does not seem to have any marked effect on the development of the pest populations except that the higher

temperatures at Bukura seem to have some depressant effect on the rate of development of *Sitophilus zeamais*. In Embu and Kisii maximum temperatures are around 25°C and minimum temperatures around 15°C. It appears therefore that temperature is not a limiting factor for pest development in any of the four areas and also that the differences are not sufficiently large to favour any one pest.

Rate of damage

Grains of maize cob samples were individually examined to determine whether an adult *Sitophilus* or *Sitotroga* had emerged. Grains which had such emergence “holes” (*Sitophilus*) or “windows” (*Sitotroga*) were classified as damaged. In this paper it is not proposed to go into any great detail of the damage analysis carried out during the experiments. What will be discussed here is the total damage caused by the two insects.

As can be observed (Fig. 1) although both pest populations oscillate around the same orders of magnitude, there is a progressive increase in the proportion of grains showing damage and therefore a gradual increase in the rate of food depletion. However this does not have any effect on the rate of development of the pest population. In all four areas the proportion of grain damage does not exceed one-fifth in the first 4 to 5 months after harvest. From then on there is an “exponential” rise and the proportion of grains damaged is in the region of one half to two-thirds of available grain. This rate of damage continues and although in the last part of the 12 month study all grains are not damaged, the frequency of grain with multiple “holes” and “windows” is increased.

Damage Interactions Between Species

It is apparent from the above that as the period of storage progresses the numbers of “new” grains available for pest development rapidly diminishes. This leads to multiple infestations of single grains. Multiple infestation of single grains by the same species is common and begins to occur fairly early in the storage period. However the situation in which grains are infested by immatures of both species is rare in the early stages and only towards the end of the storage period does the frequency of interspecies damage increase. While it is not possible to examine here all aspects of the damage interactions studied, we can see one aspect of joint damage of single grains by *Sitotroga cerealella* and *Sitophilus zeamais*. The data presented here in Table 1 shows joint damage of the two pests only in terms of the presence of immature stages of both species together. As can be seen joint damage is at still a fairly low level even 12 months after harvest at Bukura and Kisii. At Kericho and Embu the incidence of joint damage is somewhat higher and the explanation for this would seem to be that in these two places there are much less “new” grains available (Fig. 1) and so the insects have to do with the already “used” grains.

Table 1.—Proportion grains showing joint presence of *Sitophilus zeamais* and *Sitotroga cerealella* (see text 2.1.5.).

Month after Harvest	Bukura	Kisii	Kericho	Embu
11th month	0.0021 ±0.0021	0.00	0.0104 ±0.0042	0.0072 ±0.0035
12th month	0.0055 ±0.0036	0.0063 ±0.0034	0.0312 ±0.0151	0.0397 ±0.0159

Parasitism of Immature Stages of Sitotroga cerealella and Sitophilus zeamais

The parasites *Anisopteromalus calandrae* and *Cheotospila elegans* were recorded as attacking *Sitophilus zeamais*. However their level of activity was so low that no further mention is made here.

Immature stages of *Sitotroga cerealella* were mainly parasitised by *Habrocytus semotus*. A parasite known by its generic name as *Mesoplobus* was also recorded. In Kisii where immature stages of the moth were present at harvest (Fig. 1), a record was made (Table 2) of heavy parasitism of 42.86% in the third month of storage. Thereafter, the level of parasitism rapidly declined. In Bukura a 14.62% parasitism was recorded in January the fourth month of storage; this declined to 5.3% in February and thereafter died out. In Embu and Kericho isolated records of 4.69% in April and 11.43% in February respectively were observed. It is obvious from this that while a certain amount of naturally occurring parasitism is present it does not have any marked effect on the course of the pest population.

Table 2.—Parasitised immature stages of *Sitotroga cerealella* (Figures are expressed as a percentage of parasited immatures to total immatures in the population sampled).

	Bukura	Embu	Kericho	Kisii
October	—	—	—	—
November	—	—	—	—
December	—	—	—	42.86
January	14.62	—	—	3.20
February	5.33	—	11.43	1.26
March	—	—	—	3.19
April	—	4.69	—	—
May	0.77	—	—	—
June	—	—	—	—
July	—	—	—	—
August	—	—	—	—
September	—	—	—	1.17

Pest Control Measures

Although in the original experiments that were carried out first in 12 places and then in 8 places several treatments were used involving some of the newer chemicals, as dust treatments, mention will only be made here of the 2% malathion dust treatment first because this has been the standard recommended treatment in Kenya for several years and second because in this paper each type of treatment is only being considered as far as its “control action” is concerned. No attempt will therefore be made here to describe and compare the various dust treatments that were included in the experiment.

What will be described here is the control action effect of (i) the standard 2% malathion dust treatment on unsheathed maize cobs; (ii) the intact (complete) sheath cover; and (iii) the use of a fumigant in this case phosphine gas released from the use of phostoxin tablets (product of Degesch, Frankfurt on Main, W. Germany).

The Treatments

As already mentioned the 2% malathion dust has been for several years at standard recommendation for protection of stored cob maize in Kenya. The use of the intact sheath cover as a protection against pest attack has been and still is a traditional method in Kenya and in several other African countries. The treatment using a fumigant was considered because the need was felt to find out how useful a post harvest pre-storage treatment would be in controlling the pre-harvest infestation of storage insects. The phostoxin treatment was used at 6 tablets per 1000 Kg. of maize cobs. A second reason for using the fumigant treatment was to assess the importance of post-treatment infestation.

Results and Discussion

The results are shown (Table 3) of the analysis of percentage grains damaged (emergence “holes” and “windows” of *Sitophilus zeamais* and *Sitotroga cerealella* respectively) 3 and 9 months after harvest. Records were made of the intervening months but these are left out of the Table for clarity. As will be apparent there are intrinsic differences between places and as already discussed these affect development rates. However, 3 months after harvest the best treatment is phostoxin fumigation followed by 2% malathion dust. The sheath cover also exerts control. The results of untreated and unsheathed cobs are not given here but are comparable to those given in Fig. 1. All three treatments are significantly better than the control (untreated and unsheathed cobs). The phostoxin treatment is significantly the best.

Table 3.—Effects of Control Action — Percentage damage (mean ± S.E.)
3 and 6 months after initial treatment at harvest.

Treatment	Embu	Bukura	Kericho	Kisii
3 Months after Harvest				
Sheat cover	9.35 ± 3.05	5.96 ± 1.70	3.98 ± 1.51	1.44 ± 0.57
2% Malathion dust	8.47 ± 1.81	5.31 ± 2.15	1.40 ± 0.49	3.53 ± 2.03
Phostoxin tablets	6.31 ± 1.38	1.90 ± 0.42	0.17 ± 0.15	0.93 ± 0.43
9 Months after Harvest				
Sheath cover	16.94 ± 7.0	19.96 ± 3.44	29.20 ± 3.53	39.74 ± 8.40
2% Malathion dust	17.92 ± 3.25	14.13 ± 2.38	3.02 ± 0.99	15.95 ± 2.22
Phostoxin tablets	27.11 ± 5.38	22.85 ± 3.43	30.86 ± 3.76	43.10 ± 4.37

The picture 9 months after harvest is however drastically different. The 2% malathion dust is the most superior treatment and there is little to choose from the sheath cover and phostoxin treatments. The deterioration in the effects of the initial fumigation with phostoxin are already apparent in dissected samples 3 months after harvest (Table 4). Here one can see that the 2% malathion dust treatment while exhibiting higher damage (Table 3) due to emergence of initial pre-harvest infestations has a much lower population of immature stages per grain than the phostoxin treatment. The immature stages in the phostoxin treatment are a result of post-treatment re-infestation. The treatment in which the sheath covers are retained shows that while initially the sheath cover provides to some extent a physical barrier between the grain and the insect, as time goes by the insect is able to overcome this. However all treatments viz. the dust, the fumigant and the sheath cover are superior to the control, i.e., the unsheathed untreated maize cob. This can readily be seen by looking at damage levels in the 9th month after harvest in Figure 1.

Table 4.—Number of live immatures (± S.E.) per grain of *Sitophilus zeamais*
and *Sitotroga cerealella* in experimental treatments, 3 months after harvest.

Treatment	Embu	Bukura	Kericho	Kisii
Sheath covers	0.1946 ±0.1332	0.0511 ±0.0135	0.1528 ±0.0523	0.0639 ±0.0192
2% Malathion dust	0.0518 ±0.0216	0.0252 ±0.0110	0.0104 ±0.0049	0.0204 ±0.0105
Phostoxin tablets	0.2368 ±0.1126	0.0135 ±0.0047	0.0335 ±0.0091	0.0635 ±0.0191

Conclusions

In most places in Kenya the small scale subsistence farmer rarely stores grain for more than 3-4 months after harvest. It has been shown DeLima (1974) that in many areas in Kenya dust treatments may not be economical unless maize is being stored generally for more than 3-4 months. Under these conditions it would appear that the most effective treatment is the use of phostoxin tablets. It is also the cheapest in terms of cost and has the added advantage of being free of residues. Its main disadvantages are the need for some means of containing the gas for the required period and the dangers normally associated with fumigant use. However, until some technique can be developed for safe fumigation in traditional storage structures, the dust application techniques are the most appropriate for Kenya conditions.

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Action Versus Its Justification: Which Comes First?¹

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ABSTRACT

Lack of knowledge of losses in stored products retards approval of programmes to reduce post-harvest food losses in developing countries. FAO, using information recently assembled by the Senior Agricultural Advisors/FAO Country Representatives and some other sources, proposes continuing to gather loss assessment data during the execution of projects designed to reduce the losses. For example, assistance in training, widely needed, during which losses are assessed, can lead to justification for additional programmes to further reduce losses.

During the past two years, many people have focused their attention, if only briefly, on the need to reduce post-harvest food losses in developing countries. In fact we are now in a ten-year period of emphasis on such activities. Concurrently, the need to know the extent of these losses has been acknowledged generally.

To determine losses, methodology for post-harvest loss assessment must be developed, accepted and used. Responsibilities for fulfilling these needs has been focused on the Tropical Products Institute (TPI), its Tropical Stored Products Centre (TSPC), and the Food and Agriculture Organization of the United Nations (FAO), respectively, by the informal Group for Assistance on Storage of Grains in Africa (GASGA) and the FAO Governing Council and Conference. Representatives of TSPC and FAO have agreed generally on procedures for meeting these responsibilities and the criteria to be followed in assessing losses sufficiently to recommend loss reduction programmes and to evaluate programme results. Also, the Senior Agricultural Advisors/FAO Country Representatives have recently assembled information for FAO's use in meeting the overall aim of reducing these losses in developing countries.

Additional post-harvest loss reduction actions directly generated by the World Food Conference and UN General Assembly resolutions and related steps probably will begin to be requested and implemented soon.

What can we expect and be prepared for in the future? It is in this context that the question is asked: Action versus its justification — which comes first?

Summary of Experience to Date

Requests for assistance in reducing post-harvest food losses are made by governments. They contain a statement called "justification." To date these have been general statements about losses. They are of little help in and frequently seem to slow the process of gaining approval of the request. These kinds of justification, even when they include loss "guesstimates," are not the subject of this paper and will not be considered further. Justification can stem properly only from replicated data collected within the guidelines of pre-determined experimental designs subjected to the rigours of statistical analysis after which technical judgments are then made.

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² Crop Storage Pest Control, Storage Engineering, Marketing and Products Processing Officers, respectively, FAO-UN, via delle Terme di Caracalla, 00100-Rome, Italy.

Projects to assist in reducing post-harvest losses seldom have had sufficient resources of time, personnel, equipment, materials and funds to allow assessment of losses, let alone the development of methodology for this task. This has occurred for pragmatic reasons.

For these same reasons, reports to governments summarizing the results of projects have not stated the quantitative or proportional reduction in post-harvest losses achievable through the use of project recommendations, with the exception of losses reduced through improvement of milling/processing equipment where reasonably accurate judgments can be made. Similarly, data are not available to assist in evaluating the results of such projects.

Despite these facts, it is deemed that essentially all projects to assist in reducing post-harvest losses have had laudable results, though not measurable. For all practical purposes, though loss reduction has assuredly occurred, it is not presently appropriate to state that post-harvest losses have been reduced by a specific proportion as a result of development assistance.

Proposals

Some proposals for the future are made here.

Requests

In view of prior experience, it is only reasonable to assume that future initial requests for assistance will be quite similar to those in the past. FAO nevertheless will have the benefit of the use of the information collected by our SAA/FAO Country Representatives. Little cognizance will be taken, however, of reasoning such as is expressed here. Modifications are likely to come only as a result of actions by those who analyze the requests with a view to funding and implementing them and evaluating the results.

In many instances, the requests will have imprecision of a degree to require a loss survey and realistic project identification. Unhesitatingly, this need must be stated. In a way, these would be pre-feasibility or feasibility studies, a practice long used in connection with investment and which now should be practised in connection with post-harvest loss reduction.

In other instances, the requests will have adequate definition to allow further steps to be taken toward funding and implementation, but insufficient delineation of the precise activities to be conducted. In this case preparatory activities, during which a work plan is developed, must be urged strongly. The resulting plan must include necessary elements regarding appropriate post-harvest loss assessment.

In a few cases, requests will probably embody all necessary elements. Allotment of resources must then be studied to ensure adequacy for post-harvest loss assessment activities. It is acknowledged that actual and/or potential loss reduction directly accruing from training activities will be the most difficult to measure, but even here, every effort should be made to do this as soon and as factually as possible. During training, however, loss assessment is possible and should be used as an integral part of the training, one of the most important developmental requirements.

Loss Surveys and Project Identification

When loss surveys are required resources must be included to develop and/or evaluate methodology of loss survey techniques and utilize it. Such surveys, in most instances, can be expected to require at least one month and must be adequately precise and complete to allow proper justification to be stated in the project identified as a result.

In turn, projects identified by expatriate specialists must indicate the post-harvest loss assessment needs. These must be considered in development of the resulting project.

Project Document Elements

It will be necessary that certain elements in these regards are included in all project documents aiming to reduce post-harvest losses. The first of these is provision for development of post-harvest loss assessment methodology or, at a later stage, evaluation of the applicability of that already developed.

The second need is the use of loss assessment methodology to allow evaluation of the project results. This can and usually should be accomplished through comparison of proposed improvements in loss reduction techniques with each other and with existing practices. The third and related need is to provide for use of the quantified data thus obtained in development of cost/benefit data pertaining to project recommendations and alternates thereto. The benefits may be stated in money terms, or consumer or nutritional requirements.

Project Evaluation

Evaluations of projects should be considered incomplete unless they include calculations and judgments based on data derived from the use of post-harvest loss assessment methodology. These evaluations, however, must also include socio-economic and politico-economic considerations which are difficult if not impossible to quantify.

Conclusions

It is concluded that developmental assistance requests and projects to reduce post-harvest food losses and evaluations of their results will probably change little as a result of the current decennium of interest, except through efforts of specialists concerned with project identification, preparation, funding, implementation and evaluation. It is not reasonable to expect that justification of these requests will be given in terms of technically measured post-harvest losses in the foreseeable future. As post-harvest loss assessment methodology is developed, accepted, and promoted, a re-evaluation of this situation may be necessary.

The concerned specialists, however, must endeavour to the maximum to include development and use of appropriate post-harvest loss assessment methodology as one of the elements of project identification and loss surveys connected therewith. Loss assessment should occur as a part of training activities and be used appropriately to justify further loss reduction activities. In addition, the development and use of more precise methodology must be included as a tool for evaluation of project results. Also, the data so derived may sometimes be used for justification of further developmental assistance.

It is therefore concluded that actions to reduce post-harvest food losses and factual justifications of these actions will be developed simultaneously for the foreseeable future, in view of the resources of time, humans and funds anticipated to be available.

**Section 13: Pesticide Development, Management,
and Regulation;**

Section 4: Toxicology

PESTICIDE DEVELOPMENT

Organizer: A.W.A. Brown (USA)

Moderator: F.W. Whittemore (USA)

Pesticide Development: Introductory Remarks

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The discovery and development of new products, pesticides or not, is a challenging, diversified, and fascinating business; often it is frustrating, rarely it brings the elation of success. So many new products have been invented and become commonplace within our lifetime that it is impossible to look around at any moment without seeing several of them.

New pesticide development is a special case due to the time and diversity of skills prerequisite to success. It would not be stretching the point very far to say that development of only one major pesticide may approach one's professional lifetime in duration.

The poisonous quality required of new insecticidal molecules always has been measured by inventors in their search for proper use techniques. Now, such studies are becoming more a matter of regulatory law than of voluntary action by the innovator. Environmental impact may be assessed by an escalating series of laboratory and field tests, but the real evaluation comes only when full-scale practical use of the product is realized. All these and many other pre-market tests take time and as a result most new insecticides, developed for protection of food supplies, require five or ten years to achieve the first benchmark of success.

Besides time, pesticide development requires a diversity of skill not often recognized even among those directly involved. We need the imagination of the synthesist chemist to discover activity and his ingenuity to select the more effective of closely related substances, the biologist to screen chemicals for basic effectiveness, the toxicologist, the formulation specialist, the patent lawyers, and the chemical engineers to measure economics before the new candidate is even one year old. Later on, University and Government experts in field entomology or parallel sciences measure practical utility, analytical chemists discover methods to detect parent and metabolic residues, product development specialists to keep parallel investigations in balance, marketing men estimate world potentials, management commit the money for production, and engineers design and construct production facilities.

All this and government regulation, too. A reasoned government regulatory outlook may uncover overlooked needs; and unreasoned outlook may only require the same tests for all products, adding unnecessary time and money to an already burdensome load.

Finally, a new product is made, yet to succeed or fail in the face of competition, public acceptance, and maintenance of a satisfactory safety record.

To discuss certain aspects of the pesticide development process we have with us this Congress Symposium a group of speakers who have distinguished themselves in this field.

Pesticide Development — Sociological and Etiological Background

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ABSTRACT

Pesticides are primarily used in two areas, public health programs and agriculture. However, the particular geo-economic setting greatly affects the use pattern and indeed the overall attitude towards pesticides. For instance, in the pesticide and drug fields, most people high on the socio-economic cultural scale pay more attention to the inherent drawbacks than the potential benefits of these agents.

The public health problems in the Third World are enormous and frequently associated with the insects and related pests that thrive in the more tropical countries. A great deal of lip service is paid to the control of diseases such as malaria, Chagas disease and river blindness. In actual fact, the affluent part of the world is unwilling to pay much for the control of these pests, either in terms of money or technological resource allocation and the poorer countries simply cannot afford either. In the affluent areas of the world, the public health aspects of pest control are frequently dominated by recreational or even aesthetic considerations to the extent that a few flies or mosquitoes in an affluent suburban home can become targets of substantial financial expenditure. On a "per insect" basis, the allocations of resources are grotesquely skewed when one compares the wealthy and the poor.

The agricultural sector covers the entire range from intense, expensive preventive pesticide usage in the high technology agricultural countries (most noteworthy the USA) to desperate and insufficient use for survival of one-crop agricultural countries. The former are the sites of technological wealth, where all new developments and most manufacture of pesticides occur, but they are also the countries where the greatest concern is expressed (primarily by the non-user public) about environmental effects. The Third World countries are totally dependent on the highly developed countries for present and future pesticides, but their own priorities or concerns are generally not taken into consideration for obvious economic reasons. The standards of the "non-user" environmentalist are generally based on long term consequences without major consideration for short term economic penalties. The user on the other hand, concentrates on economic costs at the expense of long term considerations. (The striking analogy between pesticide development and usage on the one hand and contraceptive technology and practical human fertility control on the other has already been emphasized by C. Djerassi, C. Shi-Coleman and J. Diekman, *Science*, 196, 596 (1974)). The governmental regulatory agencies — primarily because of the pressure from the non-user community — are more concerned with safety and quasi-environmental factors; economic benefits or payback assume a very secondary role. Furthermore, the entire regulatory process in this country and in most of the other technologically advanced countries active in pesticide development (e.g. Germany, Holland; Japan, etc.) by its very nature unavoidably penalizes the innovator.

From a longer term sociological standpoint, these conflicting priorities are not necessarily bad, since stresses of this type frequently produce desirable, long term changes in society. Unfortunately, these diverging priorities coincide with a major world-wide food shortage, which is unlikely to subside for decades (see L.R. Brown, *Science*, 190, 1053 (1975)). The only real short term answer to this problem is not increased food production but rather decreased food and agricultural losses (see for instance "World Food and Nutrition Study — Interim Report", as well as "World Food and Nutrition

Study — Enhancement of Food Production for the U.S.”, National Academy of Sciences, Washington, D.C. 1975). This will require global rather than parochial outlooks by government agencies and demand decisions that need to be made over relatively short time frames. Both of these requirements are contrary to the *modus operandi* of government agencies or world wide organizations (e.g. F.A.O.). Unfortunately, rapid development (i.e. during the next decade or two) of fundamentally new pesticides will require incentives — primarily operational rather than financial ones — which neither government agencies nor the general public may find too palatable.

The Evolution of Pesticides and the Philosophy of Evolution

DR. FREDERICK W. WHITTEMORE

ABSTRACT

As the use of pesticides has expanded to truly astronomical proportions over the past 30 years, we now realize that we must consider the problems which arise from "first discovery" through pre-registration data collection to post-registration use problems and finally to the cancellation of such uses when benefits do not outweigh risks. We must ensure:

- (1) that the data required for registration is realistic and practical and that it is gathered in a safe manner,
- (2) that marketed products are safe and effective for the stated uses,
- (3) that hazards during transportation storage, use and disposal are reduced to a minimum,
- (4) that when benefits do not outweigh risks, the particular use or uses are cancelled.

In considering the assigned title "pesticide development and the philosophy of regulation" and the importance of regulations during the entire useful "life" of a pesticide, I feel it would be appropriate to expand the scope of the title to "the evolution of the philosophy of pesticide regulations". In a narrow sense, the original title could be construed to apply to the situation up to the time of first registration, although I will, in due course, return to this narrower interpretation of the subject.

Registration (for particular uses) is only the beginning and, in fact, is the "birth" of the useful life of a pesticide. At "birth" we should be concerned with safety and efficacy when used as directed.

Thus, certain regulatory standards are needed to define "safety" and "efficacy" as well as standards to develop the supporting data. Without prescribed standards for "safety" and "efficacy", definition of these essential qualities would be the responsibility of the individual producer, would vary from one producer to another, and would result in utter chaos, both in the market place and in the minds of users. Without standards for the development of supporting data, we run the risk of gathering the "wrong" data, in the opinion of the regulatory authority, and, quite possibly, exposing consumers to unrecognized hazards, in the event the "experimental" crop is consumed as food by humans or animals.

The initial registration is usually for a relatively limited number of uses. Subsequently, other uses are developed and again certain regulatory standards are required to ensure that appropriate supporting data is gathered in a safe and adequate manner. As time goes on, and the pesticide comes into widescale and general use, previously unrecognized adverse affects are sometimes identified and, almost inevitably, the relative efficacy decreases because of the development of resistance or the registration of more efficacious products. Finally, many of the uses fall into disuse and the pesticide eventually disappears from the market place. Again, regulatory authorities are required to guide the useful life of a pesticide during its declining years.

Now let us examine the "life history" of DDT and see how some of these regulatory concepts have evolved (Fig. 1).

At the time DDT was introduced in the United States we were concerned with ensuring integrity of chemical composition and we were not concerned with safety or efficacy or with post-registration problems except in so far as they pertained to chemical composition of marketed products.

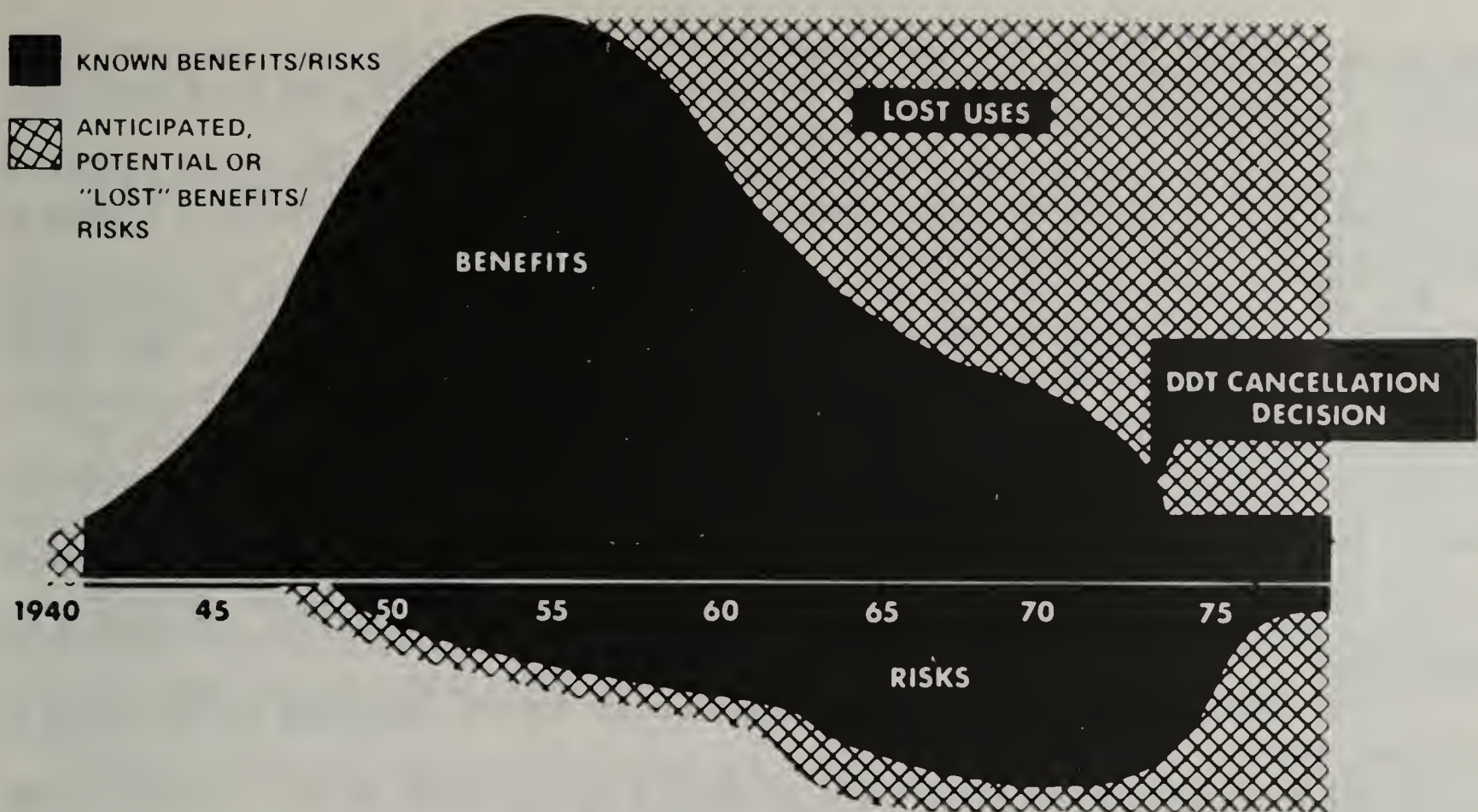


Fig. 1. –The “life history” of DDT.

In the time frame 1941/1942 we were concerned with two immediate pest control problems, one of which led to the identification of DDT as a pesticide of major military medical importance. The two problems were the control of louse-borne epidemic typhus, a major military medical problem in World War I, and the conservation and efficient utilization of pyrethrum supplies, one of the few insecticides of known value in the control of flies and mosquitoes.

The decision to allocate limited wartime resources to the manufacture of DDT was based upon two major considerations:

- (1) Laboratory and field tests showing its effectiveness against body lice, mosquitoes and flies, and, most importantly, its residual effectiveness — a property which had not been exhibited to any appreciable extent by any other insecticide up to that time — and
- (2) its extremely low order of acute toxicity to laboratory animals and to man.

The subsequent use of DDT during World War II for these purposes is well known and was shortly followed by its introduction to U.S. agriculture, where it rapidly replaced many of the older organic and inorganic pesticides for a multiplicity of purposes. No sooner had DDT come into widespread civilian use than other pesticides shortly appeared on the scene — chlordane, because of the inherent lack of effectiveness of DDT against the Mexican bean beetle, ants and cockroaches, and benzene hexachloride, primarily because of certain international finance agreements of that time — the “pound sterling” areas.

The proliferation of synthetic organic pesticides during this period led to the enactment, in 1947, of the Federal Insecticide, Fungicide and Rodenticide Act, which extended regulatory authorities to require registration of only those pesticides which could be proved to be safe and effective when used as directed.

After the passage of the 1947 Act, which required, among other things, that pesticides be registered, we began to recognize that there were indeed a number of adverse environmental effects associated with the use of DDT and the other new synthetic organic pesticides including:

- (1) the development of resistance to DDT, first by houseflies, then by mosquitoes, resistance patterns which have rapidly expanded to include over 250 species of major agricultural and public health importance throughout the world,
- (2) the destructive effect of DDT upon pest parasites and predators which, when eliminated, allowed other pests to multiply almost without check. Thus, as early as the late 1940's, the use of DDT for certain agricultural purposes was already being questioned in certain states, such as California because of these latter concerns.

However, it was not until the late 1950's and early 1960's that some of the other adverse environmental effects began to be identified and quantified, e.g., effects on fin fish, shell fish and

other forms of wildlife. During this same period, the resistance problem increased apace resulting in the search for new chemicals to “fill the gaps” left by the “lost uses” of DDT, uses which were “lost” primarily because of the development of resistance.

By 1972, concern with so-called “adverse environmental effects” had risen to such a peak that when coupled with constantly increasing resistance, finally resulted in the cancellation of virtually all registered uses of DDT in the United States.

But this is not quite the end of the DDT story in the United States. In recent years authorization has been granted for the use of DDT, where “benefits” clearly outweigh “risks” for the control of the following problems:

- (1) the Douglas Fir Tussock Moth and the pea weevil in the Northwest
- (2) the control of rabid bats
- (3) the control of rodent fleas in endemic plague areas

However, the “life history” of DDT is a typical in a number of ways:

- (1) At the time it was introduced (1942) there were no registration requirements, as such.
- (2) It was one of the first of the modern day synthetic organic pesticides to be used in the United States.

(3) The original uses were for military purposes under wartime conditions for the control of typhus and malaria.

(4) Its broad spectrum of effectiveness, persistence and low order of acute toxicity to man contributed towards the rapid proliferation of many additional uses.

(5) The rapid expansion of the use pattern speeded up the development of resistance.

(6) The development of resistance unfortunately led to more frequent and higher rates of application in an effort to control existing pest problems, thus compounding the overall adverse environmental effects of the pesticide.

In 1972, in response to a national awareness of the necessity to protect human health and the environment from the unreasonable adverse effects of pesticides, the 1947 Act was amended to require, among other things, that *all* pesticides be registered (the old Act only applied to pesticides in interstate commerce), and that all pesticide uses be classified either general or restricted. The amended Act further required that, generally, restricted uses could only be made by or under the supervision of certified applicators and that all currently registered products must be registered under the provisions of the amended Act by October 21, 1976, now extended to October 21, 1977. Finally, the Act extended regulatory authorities to the *use* of pesticides.

Now let us look at the more generalized life history of a pesticide and what regulatory authorities are now available under current law to ensure that it is marketed and used in the safest and most effective manner possible (Fig. 2).

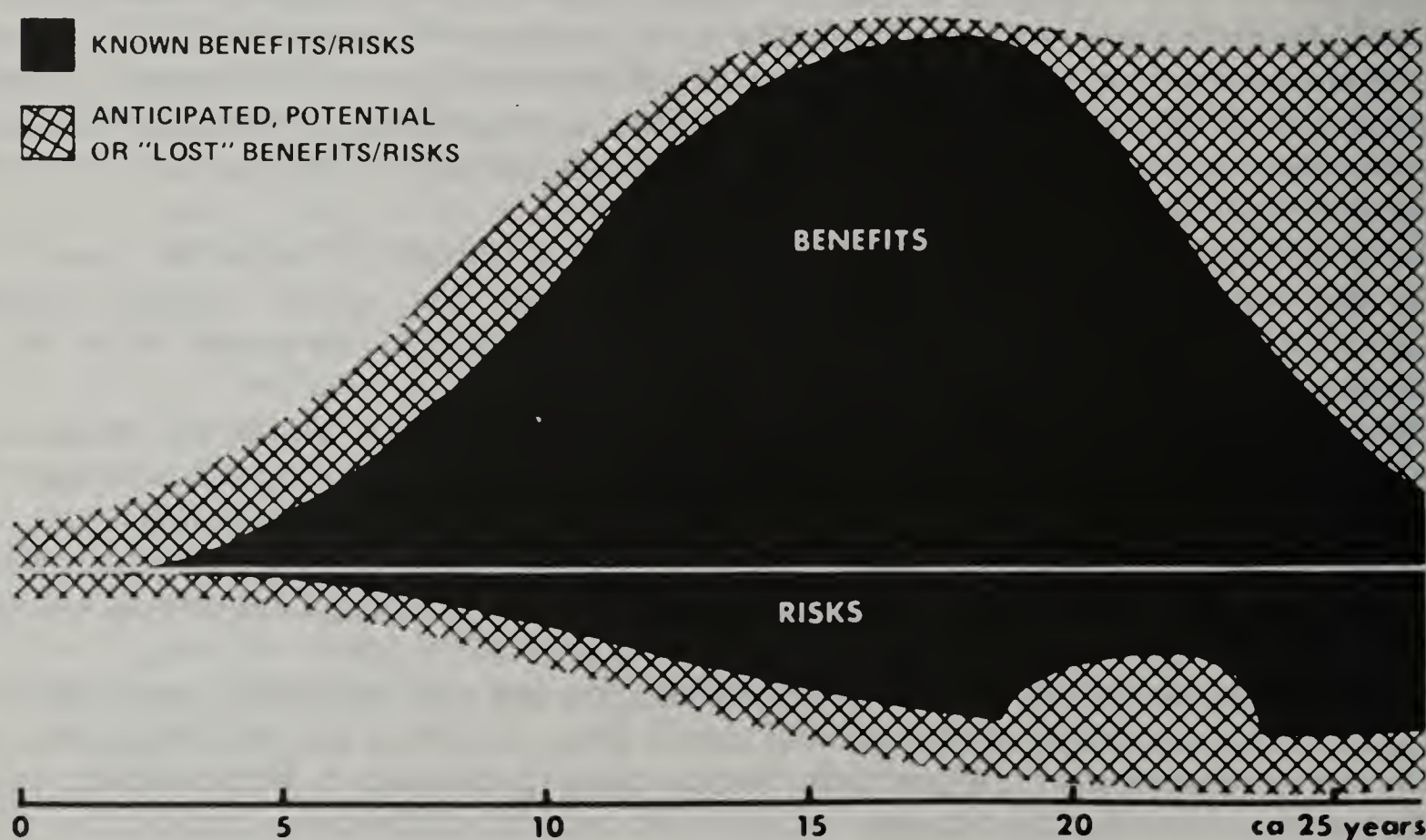


Fig. 2. –The “life history” of a pesticide

In addition to the regulatory authorities which are required to ensure chemical and physical composition of the product and safety and efficacy of each registered use, other authorities are necessary to govern the use of the pesticide during its future life.

We now realize that at the time of initial registration, neither the full scope of potential use nor, more importantly, the possible adverse environmental effects which may result from its widespread use for a multiplicity of purposes are known. And this is one of the most difficult problems facing registrants and responsible regulatory authorities. How to devise laboratory and field tests which will ensure that unreasonable adverse effects will not be encountered when the pesticide comes into widespread and general use.

We know, from past experience with such active ingredients as DDT, 2, 4, 5-T and benzene hexachloride, that moderately long periods of time must pass before some of these adverse effects are detected, quantified and evaluated. And in our efforts to minimize such effects in the future, we have developed ever more stringent registration requirements.

However, we should realize that regardless of how stringent registration requirements are made, we will never be able to foresee and evaluate all such effects in the pre-registration development stage, since, in some instances, these effects are unknown and do not become detectable until after the product is in wide-scale use.

Under these conditions, data requirements for registration should assure that the pesticide can be used safely and effectively in the light of current knowledge concerning possible adverse environmental effects. But if registration requirements are to be reduced to a minimum, both registrants and users, including those organizations representing users, must take on the added responsibility of quantifying benefits on the one hand, and detecting adverse environmental effects on the other as the pesticide comes into widespread use.

After the peak of the use of a pesticide has been reached, efficacy decreases and additional unrecognized adverse environmental and human health effects are sometimes identified, quantified and evaluated. Under these conditions, an orderly, rational consideration of the risks and benefits associated with the continuation of each particular pesticide use must be made. Such quantification cannot be made at the time of registration since it is dependent upon solid information which can only be obtained when the pesticide comes into widespread use.

**PESTICIDE RISKS/BENEFITS
AS PERCEIVED BY DIFFERENT GROUPS**

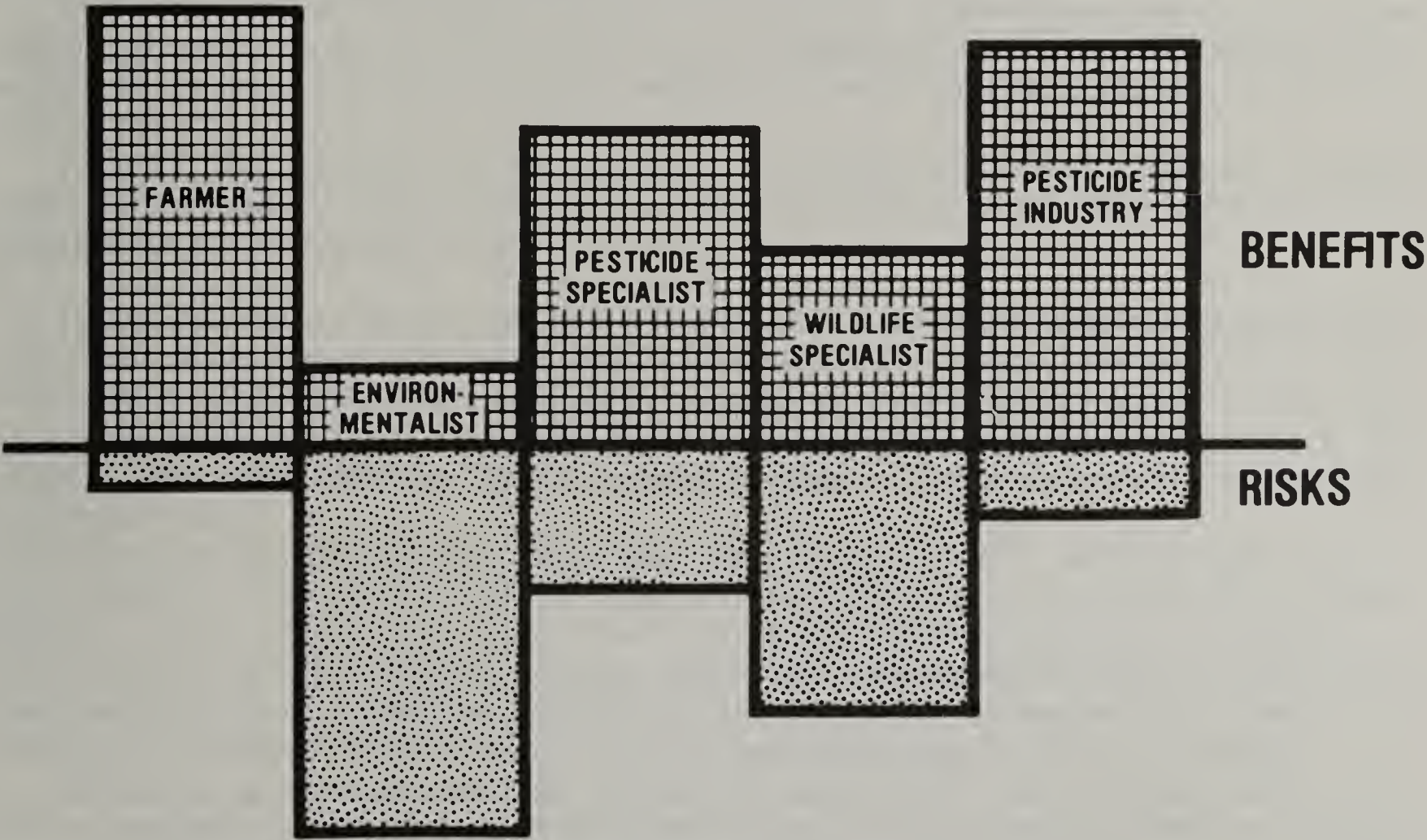


Fig. 3. – It all depends on your viewpoint.

It is during this last stage in the life cycle of the pesticide that the advisability of continuing its various registered uses comes into serious question. On the one hand, the efficacy of particular uses may be greatly reduced because of the development of resistance, the registration of more effective products, or for other reasons. On the other hand, previously unrecognized adverse effects may have been identified, quantified and evaluated. This situation leads directly into the next regulatory authority, the authority to cancel a particular pesticide use.

It is vitally important that those charged by law with making such decisions have all of the pertinent scientific facts at their disposal, a goal which can only be achieved if registrants, users and other interested organizations have met their responsibilities for gathering benefit and risk data. With such data available, risk/benefit analyses of particular uses can be performed in a satisfactory manner, although such analyses can never be performed in a purely mechanical fashion; for how can one quantify the value of a human life or the intrinsic value of an endangered species?

Recognizing that many factors of the risk/benefit evaluation can never be reduced to mathematical terms, it is not surprising that a particular risk/benefit analysis looks different to different people, as illustrated in Fig. 3.

Nevertheless, such decisions must be made in the most objective and impartial manner possible and, in the final analysis, must depend upon that rare quality known as "good judgment".

Hazards of Pesticide Development and Mammalian Toxicity: Carcinogenicity, Teratogenicity, and Mutagenicity

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ABSTRACT

The societal requirement for pesticides has created a need for a benefit/risk evaluation of these valuable chemicals in order to provide a rational policy on pesticide regulation. To provide this policy, certain exigencies in the fields of carcinogenesis, teratogenesis and mutagenesis must be defined and solved.

Although the problem of chemically-induced carcinogenesis has been established, the removal of compounds from the environment is not always feasible or advisable — thus complete safety cannot be guaranteed.

Identification of specific chemical carcinogens is complicated by the latency period, and extrapolation of data from animal models to man. Methods for estimating the latency period, and a system of animal models which would provide data that could be logically extrapolated to man is needed. The incompleteness and investigation to attempt definition of mechanisms for accumulating and/or evaluating this potentially valuable data.

The most pressing needs in teratology include: further development and use of *in vitro* testing and screening techniques, as well as, monitoring of human pregnancy and an improved cause-effect system which with present computer systems should be possible.

The determination of mutagenic qualities of pesticidal chemicals faces some of these same problems, plus some unique to the discipline i.e., the possibility of an effect which is not manifested until the F₂ or later generation(s), and the difficulty in quantitating the background spontaneous mutation rate.

Although the possibility, indeed probability, of synergistic chemical reactions is of special concern to the geneticist, it is an underlying limitation to many of today's investigative methods in carcinogenesis and teratogenesis as well.

Few people dispute the fact that pesticide technology has in large measure contributed to the achievement of our present standard of living. Accompanying the benefits, however, are many subtle and sometime gross effects that potentially threaten the health of our society. The existing implications to this and future generations demands the application of rational policies on pesticidal utilization that will enable the highest possible standard of living accompanied by acceptable risk-to-benefit ratios.

Persons suffering from an incurable, fatal disease would not wish to be deprived of treatment with a particular drug because of some vague potential danger of cancer in the distant future. Similarly, persons beyond the reproductive years certainly have less concern for exposures to chemicals that produce birth defects or genetic change than do young adults. In short, society accepts considerable risks when the risks are necessary and when acceptable alternatives do not exist, but it is predictably unwilling to accept risks when information quantitating those risks is not available.

Efficacious products are generally approved for use if there is an acceptable safety margin between anticipated residues, by appropriate usage patterns, and that level 'estimated to be safe' to humans. The toxicologist is faced with the dilemma of estimating risk to an enormous and variable

human population from small numbers of highly controlled experimental animals. Thus, there exists a considerable potential for error in assessing the risk/benefit ratio under present conditions.

Several facts which contribute to the uncertainty of toxicological evaluations should be stated clearly. There is no way to guarantee absolute safety! Small populations of experimental subjects either animal or man, provide an imprecise basis for comparison to a large human population of variable genetic/disease states, cultural backgrounds and ages. Toxicologic assessments are made singularly, while humans are exposed to a milieu. Still, it should be clearly understood that proper experimental design will minimize noise and maximize comparisons and that we are constantly expanding our toxicological armamentarium.

The development of a pesticide has two main components: efficacy and safety. It is the safety issue which I will attempt to develop in the context of the total research and development effort. Special emphasis will be placed on carcinogenic, teratogenic and mutagenic methodologies as they apply to estimating hazards in humans. I will couch my remarks toward the regulation of pesticides since it is the effort of EPA to regulate, rather than the initiative of industry, which are at issue.

Federal regulation of pesticides was initiated through the Insecticide Act of 1910. This act was concerned with the effectiveness of products and deceptive labeling practices and prohibited interstate sale of any insecticide or fungicide which was adulterated or misbranded. Regulations substantially increased in 1947 with the passage of the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) which included registration authority in order to protect consumers from ineffective products.

FIFRA was amended in 1964 to permit the denial of registration applications and in 1972 amendments completely restructured the Federal Pesticide regulatory approach from a labeling law into a comprehensive regulatory statute.

It is clear that the Congressional intent was to ensure that pesticide use was subject to a thorough human health review. The Federal Register(1)

162.2(y) defines mutagenic as "the property of a substance or mixture of substances to induce changes in the genetic complement of either somatic or germinal tissue in subsequent generations;"

162.2(bb) defines oncogenic as "the property of a substance or a mixture of substances to produce or induce benign or malignant tumor formations in living animals;" and

162.14(mm) defines teratogenic as "the property of a substance or mixture of substances to produce or induce functional deviation or developmental anomalies, not heritable, in or on an animal embryo or fetus."

Since there is no such thing as absolute safety, I will review those current documented risks due to pesticides in man. Documentation of the relative morbidity and mortality risks of the different expressions of mammalian toxicity from exposures to pesticides are imprecise. Lisella et al. (2), and Hayes (3), estimated that in 1956, 1961, and 1969, accidental deaths decreased in the United States from 152 and 111 to 87, respectively. Hayes (3) also reported that deaths due to chlorinated hydrocarbons dropped from 8.5 to 5.9 per 100,000 population while organophosphates increased from 13 to 25. The education of pesticide users, as to the toxic effects, appears to have been very successful. A look at data from two states, Florida and California, which have active prevention and reporting systems, is enlightening. Over the last 10 years, Florida has reduced accidental deaths from pesticides by 56% and California by 73%. The current estimates of total deaths in California is 2 per 100,000 deaths and 8 per 100,000 in Florida, a marked reduction from the previous 10-year average of 6 per 100,000 and 30 per 100,000, respectively. Morbidity trends are not as encouraging as mortality trends but do not demonstrate a large increase due to the shift toward the more toxic organophosphates.

The EPA paraphrases Hayes in a Federal Register (1) statement on Rules and Regulations as concluding that:

"... a rate of nonfatal to fatal poisonings of 100 to 1 or approximately 15,000-20,000 persons per year. Furthermore, of these poisonings approximately one-half involve children under 10 years with the most significant portion involving children under 5 years."

As to safety factors, the EPA states:

"The margin of safety required to render a specific injury sufficiently unlikely depends on the type of exposure and upon the persons or animals most at risk. Each type of exposure and the corresponding safety factor must be considered separately."

The EPA has characteristically applied safety factors of from 3 to 10 for those endpoints usually expressed in the morbidity and mortality tables. In summary, as previously mentioned, the acceptable

death rates due to pesticides have decreased from 30 to 8 per 100,000 deaths in Florida in the past 10 years. Nonfatal poisonings have remained constant in California and appear to be at about 5 per 100,000. There is, however, strongly suggested evidence that the number of cases is far larger than reported. Additional information on the morbidity and mortality from pesticides can be found in references 4-6.

Cancer

Regulatory action against chemicals because of their cancer-producing potential is a relatively recent procedure. It was not until the late 1950's that regulation of chemicals as carcinogens was begun. Research on the health effects of ionizing radiation yielded evidence which suggested that it would be difficult, or impossible, to demonstrate a threshold for radiation. The 'no-threshold' concept was first applied to the regulation of chemicals via the Delaney Clause of the Pure Food and Drug Act, which imposed a ban on food additives demonstrating carcinogenic activity in man or animals. Although the idea of eliminating all risks is attractive, subsequent legislation has responded to the reality i.e., in many areas risks cannot be eliminated completely without unacceptable social and economic consequences. An example of legislation recognizing the need to weigh risk and benefit is the Federal Insecticide, Fungicide, Rodenticide Act (FIFRA).

Research over the past two decades has increased our understanding of the etiology of cancer in man. Much of this research has been devoted to identifying cancer-causing substances where either laboratory or human studies have served in the ascertainment of carcinogenicity. Such identification is extremely important since many experts now assert that an appreciable proportion of all human cancer is attributable to environmental chemical factors. Indeed, it has been suggested that up to 90% of the human cancer incidence is due to environmental carcinogens. Irrespective of the accuracy of this claim, there is ample evidence to indicate that exposure to cancer-causing chemicals is a major factor in the incidence of the disease.

The simple identification that a chemical substance is cancer-causing, however, does not in every instance end the scientific and public health issue. Often, indeed too often, the chemical agent at issue cannot be completely eliminated, removed or expunged from the environment by simple legal or regulatory fiat. It is one thing to ban, through legislation and regulation, the use of DDT, for example. It is another thing to eliminate exposure to DDT. We must recognize that this widely used and environmentally stable pesticide will remain in the environment for decades, and will continue to be a source of exposure to man through migration in the water and food supply.

When a carcinogen cannot be eliminated, it is essential that we learn how to obtain information related to the exposure which might threaten public health. Only through acquisition of such knowledge, will those charged with public health responsibilities know how best to effectively regulate and control those carcinogens, that either cannot be entirely eliminated or are very difficult to eliminate, from the environment.

Without such knowledge, society and government might otherwise expend billions of dollars in an effort to eliminate a given carcinogen which, if the methods for quantitating risk existed, could prove less significant than a lifetime exposure to one-tenth of one puff from a cigarette. In this regard, I think most of us are unprepared, in lieu of persuasive evidence, to replace all the items in the home made from polyvinyl chloride plastics even though the one-hit hypothesis may imply a relatively high level of risk.

Certainly biologists and statisticians, involved in developing a strategy for risk assessment, recognize the need for methods to quantify risk in order to spare society needless expenditure of energy and/or dollars in the quest to provide a carcinogen-free environment. Such an environment can be defined as: one where the level of carcinogens present is sufficiently low that no additional induced cancer potential human carcinogen and, if so, how great an impact it is likely to have on public health.

Judgments about the weight of evidence involve considerations of the quality and adequacy of the data and the kinds of responses induced by the suspect carcinogen. The best evidence of a human carcinogen is epidemiological data in conjunction with animal tests. Substantial evidence is provided by animal tests that demonstrate the induction of malignant tumors in one or more species. This includes benign tumors that are recognized as early stages of malignancies. Suggestive evidence includes the induction of only those nonlife shortening benign tumors which are generally accepted as not progressing to malignancy, and indirect tests of tumorigenic activity, such as mutagenicity, *in*

vitro cell transformation, and initiation-promotion skin tests in mice. Ancillary reasons that bear on judgments about carcinogenic potential, e.g., evidence from systematic studies that relate chemical structure to carcinogenicity, should be included in the judgment process.

After an agent is deemed to be a potential human carcinogen, estimates should be made of its possible impact on public health at current and anticipated levels of exposure. The available techniques for assessing the magnitude of cancer risk to human populations, on the basis of animal data only, are very crude due to uncertainties in the extrapolation of dose-response data to a very low-dose levels and also because of differences in levels of susceptibility of animals and humans. Hence, risk estimates should be regarded only as rough indications of effect. Where appropriate, a range of estimates should be given on the basis of several modes of extrapolation.

Expert scientific judgments in the areas of toxicology, pathology, biometry, and epidemiology are required to resolve uncertainties about the quality, adequacy and interpretation of experimental and epidemiology data used for risk assessment.

The consideration of known and possible modes of exposure attendant to the various uses of the suspect agent are necessary to the risk/benefit analysis. All available data on factors relevant to effective dosage, physical and chemical parameters, e.g., solubility, particle size for aerosols, skin penetration, absorption rates, etc. should be reviewed. Interaction of agents which may produce a synergistic or antagonistic effect must be noted and the possibility of these reactions given consideration and/or investigated.

The known metabolic characteristics including transport, fate and excretion, and biochemical similarities to other known classes of carcinogens at high- and low-dose levels should be understood and comparisons between relevant species as well as variations in different strains of certain species noted.

Experimental carcinogenic studies should be carefully evaluated particularly as to the quality of the experimental data, and the interpretations for each study on the basis of (a) experimental protocols, (b) survival rates in controls particularly in relation to acceptance of negative results, (c) incidence of spontaneous tumors in the control compared to general laboratory experience for the same species or strain, (d) diagnostic criteria and nomenclature used for tumor characterization (additional evaluation of histological material should be obtained when appropriate), and (e) observed results of positive controls (i.e., a test group given a standardized exposure to a known carcinogen) in light of expected results.

Epidemiological studies, together with critiques of the work, with respect to its limitations and significance, will be essential to the establishing of the human carcinogenic potential. Other published critiques whether supportive human carcinogenic potential. Other published critiques whether supportive or at variance with the judgment made should be gathered and appropriately considered. A compilation of likely exposure levels with respect to longterm temporal trends, short-term temporal patterns, and weighted averages for both the total exposed populations, and for subgroups whose exposure patterns may be distinctly different from the average, should be instituted. The size of the exposed population for each of the above criteria with an indication of whether the exposures are likely to involve children and/or pregnant women, the adequacy of the methods used to estimate exposures, and the indicated range of uncertainty in these estimates must all be investigated and weighed appropriately during the decision process.

Dose-response relationships in both human and animal data should be considered whenever available, and if inadequate human data is available for characterization of the actual magnitude of risk, it should be used in interpreting animal responses in relation to human sensitivity.

The procedure for estimating the cancer risk will, therefore, involve a variety of risk extrapolation models, e.g., the linear non-threshold model and the log-probit model. Analyses should be done separately for all suitable experimental data and human epidemiological data, and the results presented in terms of excess lifetime incidence, or average excess cancer rates; where possible life-shortening estimates should also be made.

Let me at this point inject some of the thoughts of my associate Dr. Dave Gaylor and myself on the mathematical models available for application to the problem of risk assessment. A more complete discussion is found in "Reflections in Toxicology" (7). Due to, at least, the toxicological uncertainties of extrapolating risks from relatively high experimental dosages in animals to low human exposure levels, there are those who would propose complete prohibition when a chemical is demonstrated to be a carcinogen. A modification would be to use a conservative method of linear extrapolation from an upper confidence limit on the experimental result back to a zero response at

zero dosage. This procedure is described by Gross et al. (8) and the FDA Advisory Committee on Protocols for Safety Evaluation (9), and is based on the premise that at low dosages, many dose-response curves are concave upward and a straight line is a conservative upper limit to such curves.

For the particular experimental conditions, a conservative upper limit, p_o , can be estimated for any low dosage, d_o . If a threshold dosage does exist below which no tumors are produced, the true tumor rate at d_o may be zero. An objection to this method of linear extrapolation is that, in order to obtain small risk levels, p_o , the levels of d_o which could be tolerated often would be too small to make the food additive or compound (pesticide) effective for its intended purpose. However, this procedure encourages better experimentation in that, as the number of animals tested is increased, the upper confidence limit will generally decrease, thereby increasing d_o for any given level of estimated risk, p_o . The more complicated and common situations of non-zero spontaneous background and multiple dosages are discussed by Gross et al. (8).

Of the common mathematical models often proposed for extrapolation (one-hit, logistic, extreme value and probit) the Mantel-Bryan (10) procedure proposes the use of the probit.

The model for extrapolation usually cannot be determined from experimental results. For example, consider the probit, logistic, and one-hit curves which all give a 50% tumor response at a unit dose and 16% tumor response at $\frac{1}{4}$ that dose. These curves would be indistinguishable in the 8%-to-92% tumor-response range with no guarantee that either model would be applicable at lower levels. Table I shows extrapolated doses producing small risks where the experimental data appear almost identical in the 8-to-92% tumor-response range.

For example, if a dose of one unit produced 50% tumors, then a dose of 0.015 units would be expected to produce one tumor in 1,000 animals, assuming extrapolating with the probit curve. Extreme differences between models in estimated doses are noted when extrapolating to a one in a million risk. The extreme value curve, another possible model, would generally lie between the probit and logistic, depending on slopes (11). Thus, the choice of a model for extrapolation is extremely critical, the one-hit being the most conservative, and the probit the least conservative, of those examined here.

Fig. 1 illustrates procedures utilized in the Mantel-Bryan model. The Mantel-Bryan procedure uses a linear relationship between probits and log dosage. They propose a conservative slope of one

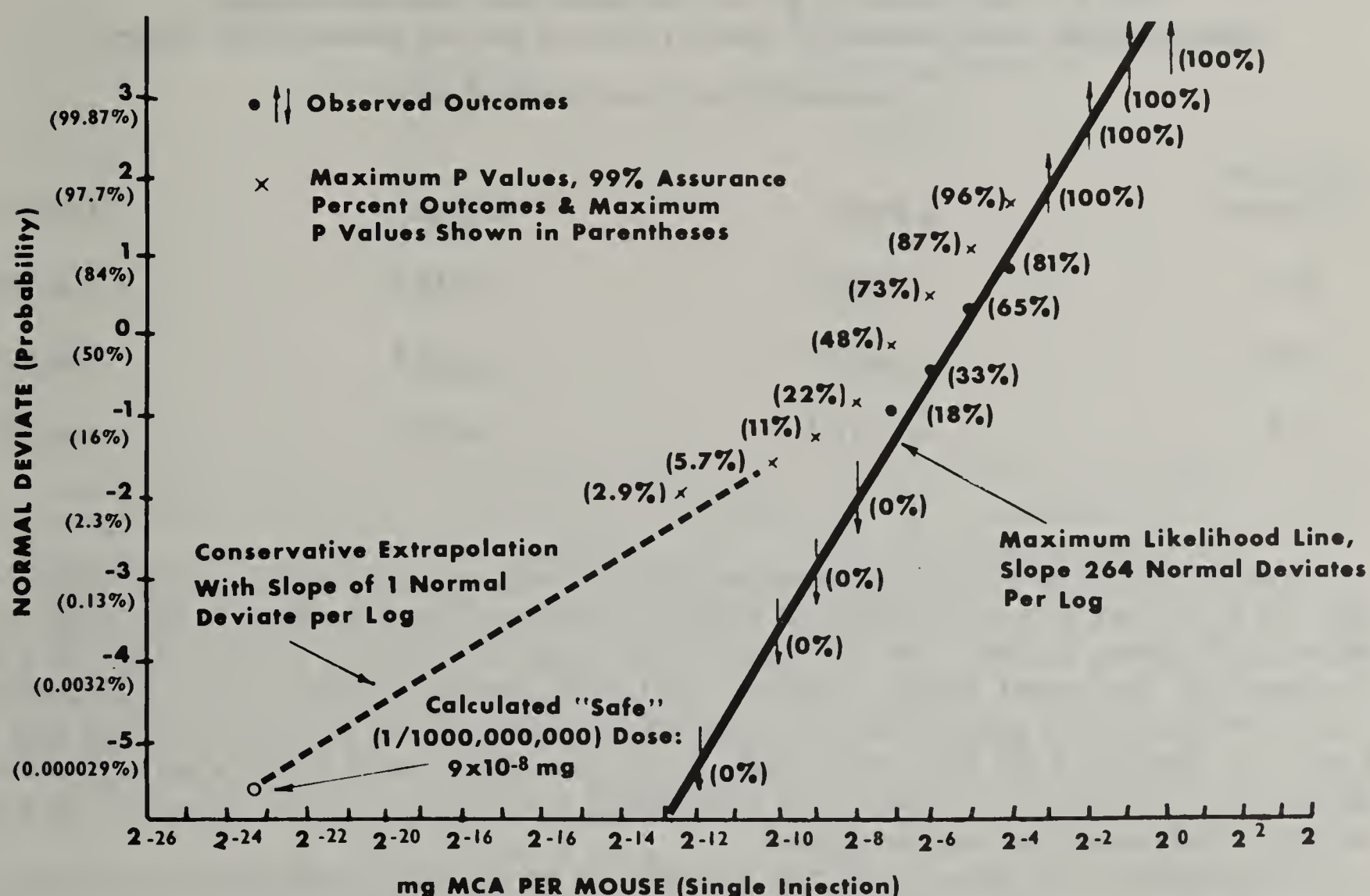


Fig. 1. —Estimation of the "safe" dose from test results with a carcinogen methylcholanthrene, at several dose levels.

probit per 10 fold reduction in dose. These lines are fitted at moderate to high responses, usually high experimental doses and generally using homogeneous groups of animals, which would be expected to produce steep slopes. There is no guarantee that slopes might not be less than one at low doses to which a heterogeneous human population is exposed. In fact, the dose-response in the smoking lung cancer data for man (percent of men developing lung cancer versus number of cigarettes smoked per day) gives a probit slope of about 0.75. However, a slope of 1, hopefully, represents a conservative slope in the dosage range below the experimental dosages. Recently, DES, alfatoxin, and cigarette smoking show slopes of 1 or less. In such cases, a slope less than one would be recommended for extrapolation.

The Mantel-Bryan procedure has these advantages: it does not require an experimental estimate of the slope; it does not require the demonstration of a statistically significant increase in tumors (which depends heavily upon the number of animals tested); it allows for a non-zero spontaneous background tumor rate; however, more research is needed where background rates are high, often resulting in treated animals with fewer tumors; it considers multiple dosage experiments. The estimated risks using the Mantel-Bryan procedure depend upon the degree of the uncertainty in the experimental data by starting the extrapolation from upper confidence limits on tumor rates and not upon proof of carcinogenicity. It is not necessary to extrapolate to a virtually safe risk of 1 in 100 million. This value was selected by Mantel and Bryan as an illustrative value which probably would not be in conflict with the intent of the Delaney Clause. Acceptable risk is a societal judgment which will have to be made by open discussions after weighing the benefit of each chemical, its possible synergism with other compounds, and the uncertainty in extrapolating from animals to man.

A dichotomous procedure could be employed by extrapolating with an extremely conservative linear model from experimentally demonstrated carcinogens and extrapolating with a less conservative procedure, such as the Mantel-Bryan procedure for chemicals not demonstrated to be carcinogens.

The extreme differences between models for extrapolating to low risks have been demonstrated in Table I. Even given a particular model, e.g. the probit, the slope was used for extrapolation produces widely different results (Table II) where extrapolations were made from the upper 99% confidence limit.

Table I—Doses required to give low estimated risks from experimentally indistinguishable results with 8-92% tumors (a dose of one unit produces 50% tumors).

Extrapolated Doses From Similar Results			
Proportion with tumors	Probit	Logistic	One-hit
10 ⁻³	1.5x10 ⁻²	3.1x10 ⁻³	1.4x10 ⁻³
10 ⁻⁶	1.4x10 ⁻³	9.8x10 ⁻⁶	1.4x10 ⁻⁶
10 ⁻⁸	4.1x10 ⁻⁴	1.6x10 ⁻⁷	1.4x10 ⁻⁸

For example, if no tumors were observed in 100 animals, one could be 99% confident that the true risk is no more than 1 in 100 million if the dose-response curve has a slope of one probit per factor of 10 change in dose, when the experimental dosage is divided by 8300. In Table II it is illustrated that the current practice of taking 1/100 of an observed no-effect level for 100 animals would provide a risk of approximately 1 in 100 million if the response curve were a probit with a slope of 2. However, if the slope were actually 1, then the estimate dose would be about 90 times smaller. Thus, not only is the choice of an extrapolation model critical, but the parameters used in the model, particularly the slope, are critical.

Unfortunately, one cannot verify experimentally the correct curve (model and slope) to use for extrapolation at extremely low dosages. It would be useful to obtain dose-response curves at levels lower than currently used in experiments. Perhaps a data bank can be accumulated for low dosage

Table II—Fraction of experimental dose using probit extrapolation with different slopes (1 probit/long = slope of 1) for an estimated risk of 1 in 100 million.

Fraction of Test Dosage for Risk = 10^{-8}		
Observed Fraction	1 Probit/Log	2 Probits/Log
0/50	1/18,000	1/130
0/100	1/8,300	1/91
0/500	1/1,800	1/42
0/1000	1/1,000	1/32

levels which provoke few, if any, tumors. Such data might eventually provide reasonable estimates of low dosage exposures, or perhaps, a check on the form of mathematical models. One difficulty would be differences in protocol employed by different investigators.

We are still faced with the uncertainties in extrapolating from well-controlled animal experiments to heterogeneous human populations. Thus, there are those who rightly contend that no method of precise mathematical extrapolation exists to date. However, as I mentioned before, using 1/100 of an observed no-effect level as relatively safe is, in fact, performing an arbitrary and crude extrapolation which ignores the uncertainty in the experimental data. Predictions of tolerable dosages from animal experiments must be made. Should these predictions be made with or without the benefit of all the scientific knowledge at hand? It is interesting to compare the Mantel-Bryan procedure with the 1/100th rule. As seen in Table III, Mantel-Bryan would set lower levels using a slope of 1 if a risk of 1 in 100 million is used. Adopting an extrapolation slope of 1.5 would be in agreement with the 1/100th rule for large experiments.

Table III—Fraction of experimental dose using probit extrapolation with a slope of one for an estimated risk of one in a million.

Observed Tumors	Fraction of Experimental Dosage
0/50	1/2,500
0/100	1/1,140
0/500	1/250
0/1,000	1/140

An important aspect of extrapolation is the choice of the dose scale. Log dosage on a per body-weight basis is frequently used as is ppm. No single choice can be recommended. The tendency is to express dosage in terms that give a nearly linear fit to the data in the experimental range.

Data in man, either dose-response or metabolic, may suggest greater or lesser sensitivity than the experimental animal. Human data seldom is available, and when available, generally it is not clear how such data could be employed in a mathematical procedure for prediction of dosages producing low risks. Much more epidemiological data is needed. A current example of this is the need to use the human data for benzidine as a component of setting water effluent standards by the EPA.

Petitioners should be encouraged to conduct experiments in more than one species. Selecting the lowest tolerance for extrapolation to man from the species tested, in order to be conservative, may tend to discourage testing in several species. This appears to be the most prudent approach. Perhaps to encourage testing in more species, the slope for extrapolation could be increased as the number of species is increased. For example, an experimental slope of 4 with a lower boundary of 3

might allow for using 1.5 rather than 1. This procedure is only a suggestion which should be investigated with existing data to determine its workability.

Another important aspect of extrapolation is determining the level of an acceptable risk. This is a socio-political decision which cannot be made by the scientist alone, but requires a risk-benefit analysis with input by many segments of society. This is an awesome task, but we are faced with it daily in setting speed limits, building codes, etc.

If the extrapolations were correct what does a risk of 1 in 100 million for a lethal tumor really mean? Approximately 1/6 of the people in the United States eventually die due to cancer. An additional 1 in 100 million would be unnoticeable. Mantel and Bryan suggested that a calculated risk of 1 in 100 million is the practical equivalent of zero since the conservative procedure used, if correct, sets 1 in 100 million as the upper limit on the true risk. The Mantel-Bryan procedure does not attempt to accept a risk of 1 in 100 million but is directed toward a zero risk not exceeding 1 in 100 million.

Some estimated risks are calculated by Friedman (12) (Table IV) using the Mantel-Bryan procedure based on a mouse intubation study for benzo(a)pyrene (13). Depending on daily intake at human exposure levels, estimated risks range from 2×10^{-5} to 10^{-6} , depending heavily upon the slope used. These data illustrate that we already may be accepting what some people would regard as a relatively high risk, 2 in 100,000, in our food supply from charcoal-broiled meat. Of course, the individual can make a choice in this instance. Such information, which is often meager and tentative, may not be available or meaningful.

In summary, the risk assessment should provide answers to the following questions (a) How likely is the agent to be a human carcinogen? (b) If the agent is a human carcinogen, what is the estimated impact on human health? I would recommend as general reading on the subject of carcinogenesis the Federal Register previously mentioned (1), and Testing of Chemicals for Carcinogenicity, Mutagenicity and Teratogenicity (14) and Guidelines for Carcinogen Bioassay in Small Rodents (15).

Table IV—Probability of tumor incidence estimated using Mantel & Bryan

Probability of Tumor Incidence Estimated Using Mantel & Bryan

Benzo(a)pyrene mg/kg/man/day	Probit Slope 1.0	Probit Slope 1.5
.010	1×10^{-6}	1×10^{-14}
.020	1×10^{-5}	1×10^{-12}
.040	2×10^{-5}	1×10^{-11}

Teratogenesis

Teratology may be defined as the science which deals with the causes, mechanisms and manifestations of developmental deviations of either a structural or functional nature (16). A teratogen may be a chemical, drug, virus or physical agent. (Some teratologists consider a gene mutation which produces congenital deformity as a fourth type of teratogenic agent; however, this will be covered later under Mutagenesis.) For an agent under test in laboratory animals to be deemed a teratogen, it must alter the structure or function of a statistically significant number of young (versus sham controls) to a measurable extent following administration of the agent: to the male before mating; to the female before or during pregnancy; or to the fetus before completion of maturation. An agent is not a teratogen if, in the absence of a dose-related structural or functional alteration, it kills developing young or causes a reduced rate of fetal growth; such adverse responses are termed embryo or fetal lethality or embryo or fetal toxicity or, collectively, developmental toxicity.

The magnitude of the problem of congenital defects is shown by the following statistics. Three percent of all children born have a congenital malformation of medical science; one-third of these

conditions are life-threatening. By age 7 or 8, approximately 10% of children have a medical problem related to abnormal intrauterine development. Over 50% of the children admitted to hospitals are there because of a congenital defect (16).

In examining a potential teratogenic agent, there are three lines of defense that should be investigated. First, is standard animal testing and chemical prediction. This was largely developed following the thalidomide disaster and includes all forms of tests carried out in pregnant laboratory animals. Doubtless, this defense has contributed to protection, but there is a belief that another thalidomide-like epidemic could occur. Hopefully, by chemical prediction and knowledge of pharmacologic action, we should be able, through better risk assessment, to avoid potential problems.

A second defense, although not fully developed is *in vitro* testing. By *in vitro* testing, I include the use of tissue culture, organ culture, whole embryo culture and emerging techniques of ova culture. Most teratologists treat *in vitro* testing as most valuable for understanding the mechanisms of teratogenesis; however, there are many who feel that *in vitro* tests for screening of mutagens and carcinogens might be highly useful in teratology.

A third defense consists of monitoring. This is necessary because the previously mentioned defenses are still inadequate. Fetal monitoring has a number of advantages. Since the congenital-defect rate in the spontaneously aborted fetus is much higher than in the newborn (16), one might assume that the fetus would provide a more sensitive indices for observing the rate of defects. *In utero* monitoring has an additional advantage of time and accuracy in determining the possible cause of insult i.e., the mother can be interviewed closer to the time of possible insult rather than 7 or 8 months after the fact. Further, should another thalidomide-like epidemic occur, a wave of abnormal fetuses might be seen as much as 6 months before the appearance of newborns with the defects.

At present, there are a number of monitoring techniques for noting defects in new borns. Although these systems probably fail to detect minor changes in brain function or long-term carcinogenesis, generally the gross physical defects are recorded. The larger portion of congenital disease is identified following infancy, since over half of the defects are not readily diagnosable at birth. Although these systems are fraught with variations due to artifacts of collecting the data, a continuous recording by time and place, and registry of congenital defects could provide important warning of teratogenic action of a new chemical, physical or infectious agent.

Another extremely important defense mechanism is that of data retrieval and utilization. It has been estimated by Larsson as reported by Shepard (17) that between 1957 and 1972 the number of scientific articles on developmental subjects doubled with about 250,000 appearing in 1972. In addition, there has been a rapid increase in descriptions of new dysmorphology syndromes in the human. Effective use of this widely spread information for solving problems related to human congenital defects is needed. A system such as the Environmental Mutagenic Information Center at Oak Ridge National Laboratory might be very useful (18). Also there is a need for texts produced from computer printouts making the material readily available to a computer user. Such books as McKusick's Catalog of Mendelian Inheritance in Man (19) and Shepard's Catalog of Teratogenic Agents (17) are good examples.

Another important concept is that of record linkage. With present computer systems, it is possible (and should be given serious consideration) to link birth records of children with malformations to pesticide exposures to the mother, or previous disease and ill health of the parent or family members. A recent preliminary report from the Kaiser Permanente System (20) used record linkage to study the association between prescriptions filled for women and serious congenital defects in their offspring.

Fig. 2 illustrates a model which might be used to prevent congenital defects. It might be conceptualized as an enzyme-type reaction with our aim being to increase the speed of the reaction from left to right. The essential portion of this reaction resides in our understanding of mechanisms. Fortunately, alert clinicians have been able to circumvent mechanism understanding and go from the human model to the final reaction, removal of a causative agent. The linkage of thalidomide and maternal rubella with specific human syndromes are examples. Unraveling the etiology of about 70% of congenital defects, whether they are due to environmental agents, developmental genes or a combination of the two, will require a concerted effort. Many animal models exist, and the emerging information on the embryo pathogenesis, genetics physiology and developmental biology of these models will be invaluable. The *in vitro* analytical methods of the developmental biologist need to be applied to our understanding of the *in vitro* mechanism reactions.

Out of our understanding of mechanisms, hopefully a reaction (Fig. 2), 3, will lead to

hypothesis testing in the human. An important co-factor for this reaction, 3a, is a basic understanding of species and genetic subgroup differences. The rate-limiting steps in this reaction appear to be located at 1a and at 3. Reaction 4 could be represented by the EPA.

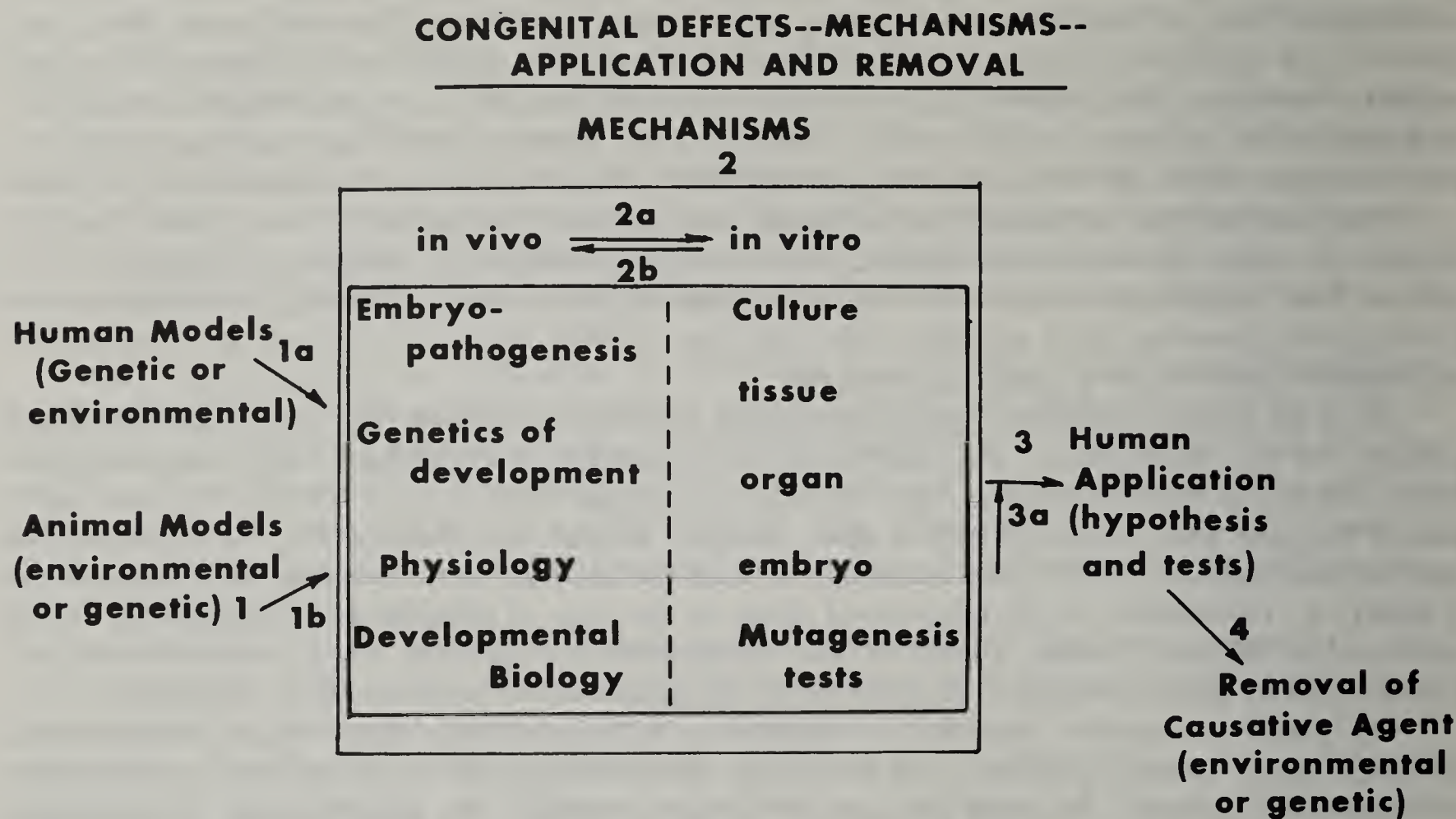


Fig. 2. –A model which might prevent congenital defects.

Examining a few of the major disasters which have occurred will provide an idea of the extent, and possible calamities which might result from either ignorance or accident.

The use of methyl mercury as a fungicide led to the widely known disasters which occurred in Japan and in the Middle East with alkyl mercury. In Japan, Minimata Bay was contaminated with mercury which when methylated, moved through the food chain and resulted in a human burden, through eating fish from the bay, which was embryotoxic, neurotoxic, lethal, and produced delayed neurologic and immunological dysfunction (21). In the Middle East, exposure was through consumption of grain treated with methyl mercury as a fungicide. The results were of catastrophic proportions, and the delayed effects are just beginning to be understood.

The wide spread use of the herbicide 2,4,5-T which contains even a small amount of the chemical impurity, 2,3,7,8-Tetrachloro-dibenzo-p-dioxin (TCDD) in Southeast Asia gave rise to a great deal of concern. Let me discuss briefly opinion as to the relative risks both to man and the environment due to 2,4,5-T with less than 0.1 ppm 2,3,7,8-tetrachloro-dibenzo-p-dioxin (TCDD) and a comparison with TCDD from other routes of entry.

TCDD, of course, is very toxic to all species studied. TCDD and other dioxins contaminate many chlorinated phenols and related products (e.g. 2,4,5-T), in addition to other materials of much wider application (at least in the past) like hexachlorophene. Why then do we worry about TCDD in 2,4,5-T? Indeed, how did we come to realize that a compound as difficult to analyze as TCDD was present in such small quantities in a commercial product which contains many other contaminants in much greater quantities?

The commercial production of 2,4,5-T was hampered in the synthetic process. Toxic effects were many including hepatoporphyrin, vascular lesions, chloracne, hirsutism and photosensitivity. One might describe the symptoms as similar to those of a modern-day werewolf, grave complexion, hairy, and afraid of the sun. The process was improved from an industrial hygiene standpoint and production continued. Courtney (22) at NIEHS studied 2,4,5-T with 27 ppm of TCDD and observed cleft-palate and cystic kidney which subsequently was described as hydronephrosis. Several other workers (e.g. Moore at NIEHS (23)) observed the teratogenicity of TCDD in the ug/kg range. There were several groups, notably DOW Chemical, that considered presence of the dioxin as the causative agent in technical grade 2,4,5-T which contained varying amounts of TCDD, but it remained for Neubert (24) to demonstrate that it required concentrations approaching 100 ppm of TCDD to

produce a clear additive effect. Even so, the controversy raged on. At the NCTR we proved, I believe, that the currently available 2,4,5-T is teratogenic in several dose response studies and that the effect is not due to a generalized non-specific effect on the maternal animal, and that TCDD plays no discernible role at the current levels found in 2,4,5-T (25).

Gehring et al. (26) showed that the half-life of a sample of 15 mg/kg dose was approximately 1 day and would be expected to plateau on repeated treatments after 3 days. This is not terribly different than what is found for rats, and was shorter than found for dogs.

Kearney et al., in 1972 (26), estimated for example that the ecological half-life of TCDD in soil is about 1 year. There is a possibility that under certain conditions the ecological half-life could be longer (conjecture only). It seems to me that there are two concerns from TCDD: (a) environmental half-life; and (b) biomagnification in grazing animals. Let's take on the ecological half-life problem first and make some assumptions recognizing that they represent over simplification of the problem: a probable ecological half-life of 1 year and an outside possibility of 10 years; 10 year's use of a product at a mean TCDD concentration of 25 ppm; and a subsequent 10-year period of use with a mean TCDD concentration of 0.1 ppm. Then, if we accept that:

$$\ln \frac{X}{X_0} = -k_1 t$$
$$\ln \frac{X}{X_0} = -(0.07) \text{ (first year)}$$

$$k_1 = \frac{0.7}{t_{1/2}} = \frac{0.7}{10} = 0.07$$

$$\frac{25 \text{ ppm}}{X_1} = \text{antiln of } 0.07 = 1.073$$

$$X_1 = \frac{25}{1.073} = 23.3 \text{ ppm}$$

What I will now do is calculate an estimate of the ecological burden over the 20-year time period (Table V).

Table V—Example of ecological burden of TCDD (over 20 years).

Year	$t_{1/2} = 10 \text{ Years}$ (ppm)	$t_{1/2} = 1 \text{ Year}$ (ppm)
a. Exposure at 25 ppm/Yr.		
1	23.3	12.5
3	23.3 + 042.0 = 065.3	12.5 + 09.4 = 21.9
6	23.3 + 094.8 = 118.1	12.5 + 12.1 = 24.6
10	23.3 + 150.1 = 173.4	12.5 + 12.5 = 25.0
b. Exposure Continues at 0.1 ppm/Yr.		
11	0.09 + 161.7 = 161.8	0.05 + 12.50 = 12.50
13	0.09 + 140.8 = 140.9	0.05 + 03.15 = 03.20
16	0.09 + 114.4 = 114.5	0.05 + 00.44 = 00.49
20	0.09 + 086.9 = 087.0	0.05 + 00.07 = 00.12

Several observations need to be highlighted:

First, at $t_{1/2} = 1$ year, 99% equilibrium occurs at 7 years at about the yearly exposure level. In other words there will never be more TCDD remaining than is in the formulation being applied. Rephrased, if you wish to predict the level of TCDD, you would take the amount of 2,4,5-T applied and multiply by ppm TCDD contaminate. If this exposure continued equilibrium would be reached approximately the end of the seventh year. However at $t_{1/2} = 10$ years, the TCDD concentration is increased to about 7 times the applied concentration after 10 years and has yet to reach equilibrium.

Now considering a continued exposure at the lower TCDD contamination level (i.e., 0.1 ppm), the rate of decrease in the improvement of the environment would only be detectable after 8 years of use if a $t_{1/2} = 1$ year, and would only be detectable after 70 years if an ecological half-life of 10 years is correct.

Also, the percentage contribution of 0.1 ppm TCDD would never be more than 1% of the residue which results in a single year of 25 ppm application. Application of a single year of 25 ppm TCDD would require 8 years to decrease to the level obtainable after continued use of 0.1 ppm TCDD. The situation of a 10-year half-life is worse in terms of what we have already done to the environment, but demonstrates a smaller relative contribution of 0.1 ppm TCDD than the $t_{1/2} = 1$ year at 25 ppm.

How about the toxicological significance of the effect of the two 10-year periods? Although the significance would vary greatly for each species, its place in the food chain, etc., again, let's consider a simplified version of possible numbers for the sake of discussion. Total the ppm x numbers of years at a ppm for a 1- and a 10-year half-life and you get 225 ppm-years for 1-10 years and 26 ppm-years for 11-20 years with $t_{1/2} = 1$ year, and 1053 ppm-years for 1-10-year period and 1209 for 11-20-year period for $t_{1/2} = 10$.

If one compares using linear extrapolation of the damage which has occurred in a 10-year application of 25 ppm TCDD with $t_{1/2} = 1$ year, it would take 2250 years of use of 0.1 ppm TCDD to produce the same "damage" as would have already been done or with a $t_{1/2} = 10$ over 10,000 years of use.

If one used an extrapolation procedure, which I believe is more reasonable, of probit analysis and experimentally produced slopes, one approaches a million years before an equivalent toxic accumulation could be accomplished. I personally believe as far as damage to the environment is concerned, this becomes even more ridiculous when we know the use of 2,4,5-T will never approach past levels and most 2,4,5-T used had more than 25 ppm TCDD as compared to the 0.1 ppm used today.

Does this mean that I am not concerned about biomagnification? It does not. Again, however, I must point out that TCDD, as an example, does have a half-life in animals, as well as in the environment and that the variance of each "system" considered is great and, in fact, frequently less than the numbers I have selected for illustrative purposes. Also, we would expect the biomagnification to be on the decline for at least 10 years utilizing the examples previously described.

I believe that dioxins in the environment are important, but I feel that pesticides will contribute little, if untoward control over the quality of production is maintained. The problem lies not with the pesticide, but with industrial chemicals escaping into the environment. As an example let me draw on data from a May 1975 article by Carter, et al. (28). Between February and October of 1971, waste oil residues of hexachlorophene production plant in Missouri amounting to about 50,000 kg contaminated with 350 ppm TCDD was sprayed to control dust. To equal this, one would have to use 400,000,000 lbs of currently available 2,4,5-T. This abuse of industrial waste disposal is not isolated and must be stopped.

Along the same line, and emphasizing the need for careful adherence to safety in chemical manufacturing is the recent explosion in Seveso, Italy. An explosion at a Swiss subsidiary of Hoffman La Roche caused a 500-gallon vat of trichlorophenol to explode (29) releasing approximately 4.4 lbs of TCDD (30). The chlorophenol is used in the production of hexachlorophene. Here it must also be remembered that in chemical reactions involving high temperatures or pressures where chlorinated phenols are precursors, the potential for forming a chlorinated dioxin exists, but not even all the tetrachlorinated dioxins possess similar levels of toxicity i.e., the 2,3,7,8-TCDD isomer is by far more toxic than the other isomers (31).

Let me finish this note with one more thought. The $ED_{0.6}$ for cleft palate for TCDD is approximately 1 ug/kg/day (23). The $ED_{0.6}$ for cleft palate is approximately 10 mg/kg/day for 2,4,5T (32).

Simply stated the concentration of TCDD would have to bioaccumulate to at least 1,000 times the concentration of bioaccumulated 2,4,5-T before the effect due to TCDD was equal to 2,4,5-T. This of course has to be superimposed on the probability of 2,4,5T being able to bioaccumulate to an effective dose level. Some good work needs to be done on the pharmacokinetics of TCDD in food stuff likely to be consumed by man and modeling of man's biological half-life.

After we have combined animal toxicology and human exposure data, we must determine if levels of contaminants actually exist in food. Great strides have been made in the last 20 years. Gas

chromatography has become a common laboratory workhorse with sensitivities proceeding from 1950's thermal conductivity (10^{-6} g), to 1955's flame ionization (10^{-9} g), to 1960's electron capture (10^{-12} g), to gas chromatography mass spectrometry (10^{-15} g).

$$\frac{ED_{06} \text{ 2,2,4,5-T}}{ED_{06} \text{ TCDD}} = \frac{10 \text{ mg}}{1 \text{ ug}} = K_{[e]} = 10,000$$

TCDD is 10,000 times more teratogenic than 2,4,5-T.

$$\frac{[2,4,5-T] + [TCDD]}{[TCDD]} = \frac{1}{1 \times 10^{-7}} = K_{[c]} = 10,000,000$$

There is 10,000 times less TCDD than 2,4,5-T.

$$\frac{K_{[c]}}{K_{[e]}} = 1,000$$

After we have determined the potential for toxicity and the presence of a residue, we are usually still faced with the necessity of extrapolating the toxic results from high doses to observed human exposure levels. This, in my opinion, is, and will remain, the greatest challenge of all.

As I mentioned earlier in this discussion of problems and advances facing the teratologist, some feel that gene mutations which result in deformity fall under the discipline, while others feel this to be in the auspices of the mutagenesisist.

Mutagenesis

I will restrict my discussion of mutagenesis, the study of heritable alterations, single gene mutations and chromosome aberrations in the DNA molecule, to genetic lesions that are transmitted to subsequent generations of the species via the germ cell. This definition excludes somatic mutations which may be involved in carcinogenesis and chromosome damage in the conceptus which may lead to a teratologic effect. Although the latter two effects are important considerations, of primary concern is the ability of a compound to cause damage transmissible via the germ cell.

The importance of mutagenesis in toxicologic research is emphasized in the definition — genetic damage transmitted to subsequent generations via the germ cells i.e., the lesion is not expressed in the organism in which the causative event occurs, but rather is first expressed in the offspring of this organism (F_1 generation). In subsequent generations, the lesion is no longer confined to the original unless the damage results in lethality or sterility before the F_1 generation reaches reproductive age.

Most of these mutational events are not observed as altered phenotypes in the first generation because of the heterozygous genotype but may be observed in the F_2 and subsequent generations. The impact of this genetic damage is compounded because it now involves individuals who have never been exposed to the mutagenic agent.

This does not imply that mutations in the heterozygous state are without effect, but only that these characteristics are expressed in the classic sense as recessive phenotypes. Upon closed examination, most heterozygotes manifest metabolic characteristics intermediate between homozygous normal and homozygous abnormal, and these individuals are capable of functioning normally in most situations, but may be more susceptible to premature aging, carcinogenesis, learning disabilities, or physiological insults. It is the realization that most mutations have a negative impact on fitness that has caused concern about unnecessary exposure to suspected mutagens.

Genetic damage can be divided into two classes: macrolesions and microlesions. Macrolesions involve a segment of the chromosome of such magnitude that it is detectable upon microscopic examination of appropriate chromosome preparations. These lesions are often referred to as chromosome aberrations.

Microlesion refers to genetic damage which may range from a change in a limited number of bases in the DNA molecule to damage of a small segment of the chromosome not detectable upon cytologic examination.

The assignment of a mutation to the macrolesion or microlesion class is merely an operational definition limited by refinements of microscopic techniques and focuses on the need for improved methodology for identifying mutagen damage.

Reports indicate mutations may be involved in many medical problems. An extensive compilation of inherited disorders (19) lists 1,876 genetic defects, the majority of which are associated with a pathologic effect.

Macrolesions, because they involve major chromosomal aberrations and gross phenotypic changes, are often expressed in the F_1 generation. It is estimated that 4% of all pregnancies are interrupted due to chromosomal anomalies (33), or conversely, macrolesions have been detected in 20-to-33% of all spontaneous abortions (34, 35). The incidence of macrolesions in preimplantation zygotes may be higher (36). It is estimated that 3-to-4% of all human zygote implants surviving the first trimester of pregnancy contain a macrolesion (34). Approximately 0.5% of all human newborns exhibit malformations which are associated with new macrolesions and the actual incidence of macrolesions is approximately 1% (33).

It is more difficult to estimate the frequency of microlesions because in the heterozygous state they are not usually manifested clinically, may affect only a limited number of bases in the DNA molecule and probably only a single abnormal protein is synthesized. Consequently, phenotypic normality may be maintained because alternate pathways may be able to compensate for any deficiencies which may occur. Secondly, it appears that most gene products in mammalian cells are present in excess of requirements for phenotypically normal metabolism; therefore, under normal conditions no effect would be readily observed in the heterozygous state (37). This does not suggest that microlesions in the heterozygous condition are inconsequential, but rather that their impact may be diffuse and subtle; nor should this imply that the mutation is not detectable by appropriate techniques.

The series of medical syndromes classified as inborn errors of metabolism reflect mutation events and have been studied regarding their genetic component. Undoubtedly as a result of improved technology, the number of detected metabolic errors has increased in the last 10 years. Over 90 inborn errors have been identified wherein a specific enzymatic defect has been isolated (38), and probably twice that many are known which are likely due to enzyme defect but have been less extensively studied (39). In some instances, several mutational events at a single locus are identifiable, forming series of multiple alleles, e.g., over 70 variants of glucose-6-phosphate dehydrogenase (40) and 40 variants of the B chain of hemoglobin (41) are known.

The incidence of microlesions in the human population has been estimated at greater than 1%, with the spontaneous (background) microlesion mutation rates estimated at 0.14 gametes (33). The mutation rate for autosomal dominant mutations is approximately 3×10^{-4} per newborn. The mutation rate of the X-chromosome (sex-linked trait) is estimated at $2.0 - 6.8 \times 10^{-3}$ per generation. The human microlesion mutation rate following radiation exposure has been estimated at 2×10^{-3} mutations per gamete per roentgen (33).

The effect of a mutation may cause lethality or sterility and only affect one generation. Alternatively, it may have only a slight deleterious influence and, thus, be transmitted to subsequent generations. There is generally an inverse relationship between the deleterious influence of a gene and the extent to which a gene is transmitted and maintained in the population. Experiments in lower organisms indicate that slightly deleterious mutations occur at least 10 times more often than those having serious debilitating manifestations (42). Therefore, in terms of risk to future generations, damage which involves large populations and less deleterious syndromes should be of concern, as well as damage which has an actual effect involving limited populations.

Chemically stimulated environmental mutagenesis is a statistical problem since environmental mutagens are not unique and their removal will not eliminate but only reduce the incidence of mutation. Improved standards of living have reduced natural selection and this, coupled with reduced incidence of infectious disease, would indicate an increased importance for medical problems with a genetic component. The major effect of mutagens will probably be to cause an increase in the load of mutations with slight effects resulting in a weaker population, i.e. one more susceptible to disease, abnormalities and frailties.

It has been estimated that 15-20% of hospital patients suffer from diseases with genetic implications and that genetic factors may account for 25% of the health burden in the United States. Lederberg (43) has estimated that a 1% increase in the mutation rate would result in an economic loss of a billion dollars annually. Several articles (34, 43-47) contain additional information concerning

incidence and cost of mutational events. It is evident, therefore, that mutagenesis is not a scientific curiosity but relevant to the health concerns of the human population.

The ability of radiation to cause mutations in lower organisms was reported in 1927 by H.J. Muller, and the ability of chemicals to cause mutations was shown some 20 years later (48). However, it was not until the 1960's that concern associated with human exposure to environmental chemicals and resulting mutagenesis was widely expressed. This concern was reflected in the MRAK Report (44).

The scope of the problem of environmental mutagenesis is related to the extent of potential human exposure, the length of the latency period between mutation and detection of mutation, and irreversibility of the damage. It is estimated that the human population is exposed to 500 new commercial chemicals per year. Some of these chemicals, e.g., drugs, involve limited populations; other chemicals, e.g., pesticides and automobile-exhaust pollutants, result in much greater human exposure. In the United States, because of efficient distribution system, close to 100% of the population may be exposed to a chemical shortly after its development. Further, the annual use of synthetic organic compounds in the U.S. is approximately 55 billion kg of over 1,000 different chemicals with an annual rate of increase of almost 15% per year.

Many suspected mutagenic agents have been detected in water, air, soil and food of which all serve as a source of human exposure. Therefore, it must be concluded that human exposure to various classes of chemicals, including potential mutagenic agents, is extensive. These agents may enter the environment through (a) intentional or unintentional release during synthesis, (b) distribution of chemicals, (c) biological transformation of inert compounds, or (d) naturally occurring components of a biological system.

Although few compounds have been shown to be mutagenic to a mammalian species (probably due to inadequate data), the list of chemicals known to be mutagenic in available test systems is substantial (49-52). Various compounds representing such classes as alkylating agents, azo dyes, epoxides, aflatoxins, phosphoric acid esters, nitrosamines and polycyclic hydrocarbons have been shown to be mutagenic by at least one criterion. Many of these compounds are also carcinogenic and/or teratogenic, and they are components of the human environment.

The effect of mutagenic agents on the decision making process of society today can be summarized as follows:

1. Most mutations are deleterious, ranging from the extreme, sterility or embryonic death, to such harmless effects as changed hair color.
2. The effect of mutagenic compounds is statistical; i.e., they increase the incidence of mutation above an already occurring background rate.
3. Detection of an increased mutation rate in humans usually does not identify the causative agent. Since it is not possible to treat the cause of the phenotypic expression or prevent its transmission to subsequent generations, prevention of an increase in the mutation rate is the only practical protection of the human population.
4. Since many compounds which are beneficial to the human population are suspected mutagens, accurate assessment of mutagenic potential is important for cost/benefit and risk/benefit decisions.

Mutagenic compounds present potential hazards to the health and welfare of human populations. This risk to future generations, although difficult to quantitate, must be considered.

The problems of detecting potentially mutagenic compounds, the state of knowledge concerning mutagens, and the problems of relating this knowledge to risk in human populations have been extensively discussed and several reviews are available (32, 46, 53-55). These discussions generally focus on the inability to quantitate mutagenic potential because of lack of adequate methods and data. Programs are necessary to develop methodology whereby EPA can carry out its regulatory responsibilities as related to potentially mutagenic agents.

In order to complete this mission, it will be necessary to: (a) develop new predictive test systems, (b) obtain quantitative data in various test systems, (c) determine factors influencing mutation frequency, and (d) determine mutation rates in humans as a basis for evaluation of test systems.

Conclusion

Underlying this discussion of carcinogenic, teratogenic and mutagenic research are certain basic premises. First, the present society must continue to exploit our pesticide technology if our standard

of living is to be maintained. It must be recognized that these chemicals carry a risk, as well as, a benefit, and play a role in changing human disease patterns — a role that needs to be better documented. In addition to documentation requirements, efforts to correlate disease with exposure needs to be emphasized. Finally, is the need to develop methodologic and/or modify existing techniques in order to better determine the agents and the mechanisms of these agents that have a causative carcinogenic, teratogenic and/or mutagenic effect.

I perceive the development of pesticides much as a parent must the development of social awareness in a child. Starting with the development of DDT, the modern pesticide chemical era was born. The years of childhood were a rapid progression of discoveries. The world was characterized by growth and a forgiving family — quick to overlook indulgences, mistakes, and intraspective behavior, while proud and pleased of exploits and accomplishments. The period of adolescence or youth was a period where the exuberance once encouraged was more often than not met with controls, questioning and a sudden sense of disapproval. Ubiquitous favor happened to be suddenly replaced by unwarranted condemnation of past behavior and actions. Inattention to acquiring some of the required prerequisites of a responsible adult, living and working in a complicated world, became a redundant theme of an ever growing group of critics.

The young adult would find some of the early years frustrating. Rectification of some of the mistakes of the past would take time-resources away from the rate that new potentials could be developed. Where cases of unacceptable behavior, by the new adult standards, were documented — distrust and exclusion replaced the encouragement and praise once lavishly awarded.

We are now at the age of the young adult capable and needed by society. The question is whether the maturity and responsibility are present to allow the documentation of a record of dedication aimed toward removing the deficiencies of the past preparations, making the sacrifices of short-term advantages while building the credibility for a long-term community service with the rewards due to the respected citizen.

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Pesticide Developments and the Question of Side Effects and Environmental Hazards

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Chemicals used in agriculture for the protection of crops are practically as old as systematic planting. Seed treatment with arsenicals goes back to 1640, the fungicidal activity of sulfur against soil insects and fungi dates from 1653 and fungicidal treatments with calcium hydroxide have been undertaken since 1697. Copper sulfate for seed treatment of small grains was used in the 18th century while copper-arsenicals were applied for Colorado beetle control in the U.S. in 1868.

Together with these inorganic chemicals; a number of plant extracts such as nicotine, derris, or pyrethrum formed the whole arsenal of pesticides until 40 years ago.

Most of the inorganic pesticides used up to this date had some very serious limitations and, both from the standpoint of toxicology to humans and to the environment, their drawbacks became more and more evident. Together with the growing world population and the austerity programs in a number of countries concerning food supply a stimulus was created to increase agricultural production in the mid-thirties.

Dinitrophenol derivatives were among the first synthetic organic chemicals which found a use in agriculture as insecticides and ovicides. But, like the inorganic chemicals, they had a number of side effects: they showed a high mammalian toxicity and they were skin-irritating and staining. Immediately before World War II, some polynitrated carbazol derivatives, which were available through Hoechst in Germany, could successfully replace arsenicals for some uses.

Both in the fields of herbicides and fungicides, the situation at that time was similar: a few inorganic chemicals such as sulfuric acid or chlorates were used for weed control, and sulfur and copper respectively were the basic ingredients to prevent the growth of fungi. This ended the first phase of pesticides in which inorganic chemicals with mostly limited performance with many undesired side effects were dominant.

Two chemical groups, the DDT-type chlorinated hydrocarbon insecticides and the 2,4-D-type hormone-like weedkillers, initiated a second phase some 40 years ago and revolutionized the scene of agricultural chemicals.

In the case of DDT, the spectrum of activity was so large that this chemical could not only be used for the control of many insect species on a wide variety of crops but found, and still has as its main application, the control of vectors of endemic diseases. But, despite this broad spectrum, a few insect species and most acarines could never be controlled successfully by DDT and a number of insects, harmful to crops or simply nuisances, developed resistance to DDT only a few years after its introduction. As early as 1948, houseflies developed resistance to DDT, so that it became clear that although DDT was a very considerable step forward, there was room for further developments.

When the chlorinated phenoxy acetic acids were announced in the U.S. in 1944, a new era in selective weed control was opened in a variety of important crops such as small grains, corn, etc. UK researchers had detected a similar chemical, MCPA, which is the 2-methyl analogue of 2,4-D, in 1936. This chemical, which found a wide application especially in Europe, is somewhat more tolerant to small grains than 2,4-D. This group of chemicals proved to be as well from the standpoint of selectivity as from the toxicological and environment point of view a real progress.

Let us choose now a few examples which can stand as models for development of pesticides in the last four decades. The selection is arbitrary and stems primarily from my acquaintance with the company that originated these chemicals.

DDT

As the development of DDT is so extraordinary, it may be taken as the first example: When P. Müller synthesized in fall, 1939 his compound 1139, later DDT, he found that it had a surprisingly high contact activity coupled with a good residual effect on houseflies. He confirmed his findings on a number of other insects such as aphids, mosquitoes and Colorado beetles. 18 months later, the first official application was made by Wiesmann in one of the two Swiss Federal Agricultural Research Stations. In 1941, some DDT preparations were sold in Switzerland under formulation numbers, but the real introduction of DDT for the control of a large number of insect problems in crops occurred in Switzerland in April 1942, exactly 2½ years after the first screening tests had been carried out. In fall 1942, the introduction of DDT for fly control in barns began and the marketing of DDT for lice eradication on humans took place about at the same time.

What was known on side effects and potential environmental hazards when this pesticide was introduced into agriculture and vector control?

When Domenjoz started his first acute and subchronic toxicity studies on different laboratory animal species, he immediately realized that the formulations of DDT-products had a profound influence on the toxicity. Oil formulations were 2 to 8 times more toxic than aqueous suspensions when applied orally. For dermal applications, the differences in toxicity between aqueous suspensions and oil solutions were even more pronounced: dermal applications of dusts of aqueous suspensions proved to be quite safe for animals and human beings.

Geigy's findings about performance and toxicity of DDT were transmitted in 1942 via diplomatic channels to representatives of various countries participating in the war. Samples were transmitted to the respective governments so that as well in the plant protection as especially in the vector-control field test work was started immediately afterwards. Due to the efforts of thousands of research workers, it was possible that in 1943 several campaigns could be launched, of which the successful eradication of the typhus epidemic in Naples during the winter 1943/44 became best known.

The international introduction of DDT preparations for crop protection took a little more time. Residues on edible crops were of no concern at the time of the early applications on fruit, vegetables, etc., in most countries. Tolerance levels for pesticide residues on food were issued for the first time in the U.S. around 1947, based on the Federal Food, Drug and Cosmetic Act. They served as a guide for the establishment of similar legislation in other countries. The level of 7 ppm was primary based on existing tolerances for arsenicals. A more sophisticated control of pesticides only became possible after analytical chemistry was able to offer new and much more sensitive methods. Chromatographic techniques reached such a degree of perfection that residues in the order of parts per trillion could be analyzed while analytical methods available during the first years of the use of DDT were mostly unspecific, their sensitivity being in the order of 1 – 1/10 of a part per million.

Early chronic feeding studies with DDT in laboratory animals had shown that with small dosages accumulation occurred. However, when higher dosage rates were fed, this accumulation did not continue indefinitely but stopped at a level which was still far away from being toxic for the test animals. These findings gave a further assurance that apparently in the animal a metabolism of DDT occurred leading to metabolites which were gradually excreted.

The success of DDT was such that amounts in the order of 100,000 tons per year were produced and applied for a period of about 10 years. The fact that — at least at the beginning of the WHO-malaria-control-programs — DDT was not only used on the inside of human dwellings in tropical countries but also on lakes, rivers, ponds, etc. for mosquito-larvae control, that large forest areas were treated with DDT from the air, that stocks of formulated DDT of the armed forces were dumped into the sea, led to an ubiquitous distribution of DDT.

At the time Miss Carson wrote her book, DDT and other chlorinated hydrocarbon insecticides had been used with great success for nearly 20 years. The side effects she described stemmed mainly from misuse and accidental spillage and concerned a small number of fish and birds species only. Her conclusions based on these facts were drawn basically by extrapolation. But the book had at least one positive effect: a lot of scientific studies were undertaken as a consequence. Out of those studies a

very significant result came to light, namely the bioaccumulation of DDT and other chlorinated hydrocarbons in the food chain. Woodwell could demonstrate that in a salt marsh sprayed with DDT, considerable amounts of DDT and metabolites could be found in the mud of the marsh. While the water had a concentration of 0.005 ppb of DDT, Plankton had a 1000 fold higher concentration. Shrimps, crabs, fish, etc. accumulated amounts which were 10 times higher while birds could store DDT and metabolites from a few parts per million up to an extreme value of 75 ppm. It goes without saying that accumulations in that order of magnitude were alarming. These observations have, however, to be evaluated in the proper perspective. Most of these findings are confined to limited areas, they are practically limited to aqueous systems only and are mostly occurring to bird species which eat primarily fish of such polluted regions. It has to be stressed here that residue determinations prior to 1965 are practically completely useless as the analytical methods applied prior to the application of chromatographic techniques did not differ between DDT and other chlorinated hydrocarbons including PCB's.

Wurster showed in 1968 that concentrations of 1 ppb of chlorinated hydrocarbon pesticides were able to inhibit photosynthesis on some species of algae. It is not conceivable, however, that concentrations like this could ever occur in the open sea, and even in salt marshes as discussed before, the water concentration was 1/20 of the rate which caused the inhibition. The conclusions Wurster drew from his investigations proved to be invalid.

So, in spite of the wide use of DDT, the side effects have to be evaluated in the light of its positive effects as well, and then it becomes evident that the benefit/risk formula speaks in most cases for and not against DDT.

There remains one problem to be evaluated: Is DDT carcinogenic to man? Several generation experiments on selected strains of mice at dosage levels from 2 to 250 ppm resulted in liver cell tumors. Feeding tests with monkeys over a period of 6 years with 10 mg/kg of DDT applied 5 times a week, which corresponds roughly to 150 ppm in the diet, did, however, not produce any clinical symptoms, nor did any fatty livers occur. The cross sectional epidemiological studies on workers exposed to DDT and observational studies on volunteers did not lead to cancer or were too limited and/or too short to allow any conclusions to be made regarding carcinogenesis. This is the status after more than 30 years of intensive use of DDT in agriculture and vector control.

Scientific developments continued and around 1950 it became evident that a number of important insect complexes could not or no more be controlled by chlorinated hydrocarbons and that new insecticides were badly needed. In contrast to DDT, where the performance was the only goal for the research workers, this time performance *and* toxicology considerations stood at the beginning of their new research projects.

Diazinon

When chemicals were screened it was silently understood that this was a process of an evaluation of selective toxicity. The first thiophosphate — parathion — which was of real importance for agriculture, was introduced in 1948 by Bayer. In comparison to the chlorinated hydrocarbons of the DDT-type, it had a considerably higher acute toxicity. The goal of research workers in the early 1950's was consequently to find phosphates with lower toxicities than parathion and the like. The lower stability of phosphates and thiophosphates in comparison to the chlorinated hydrocarbons made an accumulation in crops and animals a priori unlikely. The degree of instability of some phosphates was so high that — although they were per se active against insects — they could only be used in a very limited way commercially. Diazinon, a heterocyclic thionophosphate, proved to be a compound which had a considerably lower toxicity than parathion (300-800 mg/kg LD 50 in comparison to 10-15 mg/kg in rats). Being a thionophosphate, it is activated by oxidation procedures to form its oxygen-analogue Diazoxon. Krüger found in 1960 that high levels of Diazoxon are found in susceptible insect species while mammals are able to hydrolyze and thus detoxify both Diazinon and its oxygen-analogue likewise.

Diazinon found and still finds a wide use as insecticide in fruit, rice, corn, vegetables, etc. and household and garden products. In balance studies, Esser et al. showed that Diazinon has a biological half-life time of 12 hours in the rat and that hydroxypyrimidine — as the number one metabolite of hydrolysis — is further oxidized to less toxic hydroxylated pyrimidines. In contrast to DDT, where DDE is more persistent and more toxic, the Diazinon metabolites are detoxified fractions of the original molecule and do not cause problems for the environment.

The third phase of development of insecticides brought a number of new chemicals with new activities, with reduced persistence and with more selectivity. Their acute toxicities were of varying order of magnitude, but due to their lower stabilities their long-term effects on man and the environment are of no practical concern.

Let us take now an example of a herbicide. Weed control in crops has to be made if possible only once per season so that compounds of a low persistence like phosphates are of limited practical value.

When compounds of higher stability will be applied to crops, they have to stay there for a period of time and consequently their disappearance in the plants or in soil is of primary interest. In addition to biological activity, toxicological *and* environmental considerations played a very important role in the selection of new herbicide candidates right from the beginning of our investigations.

Atrazine

Atrazine is chosen as model for such a group of agrochemicals. Chloro-s-triazines of the Atrazine-type are in wide use as selective weed-killers, especially on corn. They can be applied pre-emergence, that is on bare soil, and post-emergence on the crop. The root system of crops as well as of weeds primarily take up Atrazine, but a significant part enters the plant through the leaves as well. Corn is able to metabolize Atrazine as fast as it is taken up. Thereby, a cyclic benzoxazinon-hydroxamate, which is naturally occurring in corn, is primarily responsible for the metabolism. In plants, peptides and amino-acids form conjugates with Atrazine or its metabolites which are no more phytotoxic.

In soil, micro-organisms — both fungi and bacteria — are able to metabolize triazines as well. Thereby, dealkylation with or without side-chain oxidation are the degradation pathways. A further inactivation of chloro-bis-alkylamino-s-triazine-herbicides is due to a binding on soil particles.

For other triazines, especially for the 2-methyl-thio-bis-alkylamino-s-triazines of the Ametryne-type, the cyclic hydroxamates do not play any role in the detoxification process. However, Ametryne is also metabolized as well in the plant as in soil to the respective hydroxy-analogue. In addition, oxydative processes, both at the methylthio group as well as at the alkyl side-chains, and dealkylation of the alkylamino groups are responsible for the deactivation of this group of triazines.

It is understood that a pre- or post-emergence herbicide has to have a reasonable stability so that temporarily concentrations of unmetabolized triazines can be found in the soil while crops, which are resistant enough for selective weed control, do not have at harvest any significant amounts of unchanged triazines.

With the triazines, we have a group of chemicals which is widely used in agriculture today. Their mammalian toxicity is in the order of 2000 mg and less. When applied to soil as pre-emergence herbicides, they cause a temporary pollution of the environment, but they are metabolized to a large extent during the growing season by plants as well as by soil micro-organisms. Even with dosage rates considerably higher than those used for selective weed control, no accumulation in soil could be found. This example demonstrates that even relatively stable compounds can be applied in agriculture without causing harm to crops, without leaving residues on their edible parts and without interfering more than temporarily with the environment. However, even there they do not negatively influence the soil organisms and thus change the biological equilibrium.

It has to be stressed that the studies, which had to be made to reach that conclusion, are not only time but also money consuming. The present knowledge on triazines would have been impossible without the progress reached in analytical chemistry including tracer techniques and without the improvements in biochemistry. It is my firm belief that agricultural science has reached a level which offers the maximum of safety to man *and* the environment. Efforts to go beyond this level would most unlikely increase the safety pattern significantly but definitely would increase the cost in a way which may preclude any progress in the development of new pesticides.

Pesticide Development and Needs in Developing Countries

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ABSTRACT

During the period 1963-73 the total use of pesticides world-wide has more than trebled, but in 1973 all developing countries together utilized only about 8 percent of the total world pesticide production, and 85% of it was employed in the control of public health vectors and on industrial export crops, such as cotton. Shortages and soaring prices in 1973-74 had a serious retarding effect on pesticide use and adversely affected crop production in developing countries. Past pesticide use and projected requirements in 38 developing countries are discussed. Large increases in use levels appear necessary before a real impact is felt in food production through a significant reduction in pre- and post-harvest food losses. Past experiences and current dilemmas faced by governments in approving compounds for local use are reviewed. Pesticide legislation and quality control at the national level are recognized as essential initial steps in promoting the efficient and safe use of plant protection chemicals. Developing countries generally are anxious to encourage the establishment of local pesticide formulation facilities, based on feasibility studies.

In spite of a variety of problems associated with the use of a number of compounds, it is an indisputable fact that pesticides have made very substantial contributions to the expansion in agricultural productivity that has occurred in recent years, mainly in developed countries. As we know, pesticides frequently offer the only means of arresting disastrous crop losses, and in many areas production today would be quite unprofitable without them. Therefore, if drastic curtailment of productivity is to be avoided, then it is inevitable that pesticides will continue to be widely used for many years to come. In fact, grossly insufficient and/or inefficient use of pesticides and other plant protection measures, in most developing countries, have been responsible for an average loss of more than 30 percent and in many instances more than 50% of potential crop yield. In this connection, in 1974, combined pesticide use in all developing countries put together has been estimated at less than 8% of world pesticide production, which is less than that used in Japan alone — and this is in spite of the fact that developing countries represent approximately 72% of the total utilizable land, world-wide.

The importance of these figures should be seen in conjunction with an estimate, made in the documentation for the World Food Conference in 1975, that by 1985 the pesticide requirements of the developing countries would have to increase *fivefold* over 1970/71 levels before a real impact is felt in food production, through a significant reduction in pre-harvest and post-harvest food losses.

Shortages and soaring prices of pesticides in 1973-74, which were related to the so-called “energy crisis,” prompted the Economic and Social Council of the UN and later the World Food Conference to request FAO, in cooperation with WHO, UNEP, UNIDO and the pesticide industry, to review the entire subject of pesticide needs, in the context of overall plant protection requirements and their potential effect on food production in developing countries. As a result of these requests, and as a first step, FAO undertook a preliminary survey to determine demand trends, both current and short-range, in relation to past use. Based on the experience gained, a permanent system was to

be developed on pesticide supply and demand, with the basic objective of locating both deficits and sources of supply, possibly to be coupled with emergency funding arrangements, whereby developing countries, and especially those most severely affected, could obtain appropriate pesticides.

The first survey was initiated in September 1974 by sending a questionnaire to 99 governments seeking information on:

- I. Past pesticide consumption for 1971 through 1973 on a) herbicides, b) insecticides, c) fungicides (classified by broad chemical groupings and subdivided into preparations manufactured/formulated locally and imported) and on
- II. Estimated pesticide requirements for 1975 through 1977.

A brief evaluation of the data received might be of interest. The pesticide consumption reported by 38 countries for 1973 totaled 160,000 metric tonnes of which 106,000 tonnes was insecticide, 49,000 tonnes was fungicide and less than 5,000 tonnes was herbicide.

It is interesting to note that consumption of all pesticides had increased from 107,000 tonnes to 160,000 over the 3 year period 1971-73, representing a 23% compound rate of growth per annum.

Overall, only about one-tenth of the increased supplies had come from domestic formulation, though this varied considerably by class of pesticide and by country.

From this sample of 38 countries, it seemed clear that increases in consumption of pesticides during the 1971-1973 period far outstripped earlier industry estimates of 10 percent per annum. Herbicides, although used in very small quantities, showed the most rapid rate of increase (32% per annum), while insecticide use grew at the slowest rate (21%). Fungicide use expanded at a rate of 25 percent per year, over this period.

The rapid rates of increase in demand for chemical pest control in developing countries is due in part to the fact that pesticides in general, and herbicides in particular, are relatively new agricultural inputs for most countries. As such, their full potential for increasing crop production remains relatively unexploited.

In developing countries of Central America, where pesticides have been available for a relatively long period, the overall rate of growth in pesticide use (17% per year) was lower than in Asia (35%) or South America (22%). As pesticides have been a relatively newer input in the developing countries of Asia, it can be anticipated that their future rates of growth will continue to exceed those of South and Central America. The African countries surveyed demonstrated a net decline in pesticide use during the 1971-1973 period. This was most likely due to a lack of available supplies and foreign exchange, rather than a decrease in demand. The African countries surveyed are completely reliant on importation of formulated products. Lacking any domestic formulation capabilities or established purchasing patterns, to assure priority allocation, these countries were relatively harder hit by the supply shortage in 1973-74 than developing countries in other regions.

Increases in the rate of consumption of herbicides exceeded those for all other classes of pesticides. This was due in part to the rather recent introduction of high-yielding varieties of rice and wheat, which are more reliant on fertilizer and weed control than traditional varieties. Recent data received from some of the developing countries indicates that yield from fertilized, high-yielding wheat varieties was depressed from 30 to 80 percent when these were not treated with herbicides for weed control. Similar data has been received for rainfed rice in Africa and Asia. Due to the dramatic yield response associated with chemical weed control, rapid increases in demand for herbicides are expected to continue through the current decade.

The uncertain international economic situation which has led to highly variable international and domestic prices for agricultural products, as well as most other items which compete for foreign exchange, has exerted a dampening effect on intentions for future pesticide consumption. As a result, the overall rate of increase in use, within those countries responding to the FAO questionnaire, dropped from 23 percent per year for 1971-1973, to an anticipated 9 percent for 1975-1977. However, this has now been revised to 15% and the final figure might well be closer to 20%.

Since pesticide manufacture is a high technology industry, nearly all primary manufacture is confined largely to industrial countries. Although a small and gradually increasing amount of final stage manufacture is occurring in a few developing countries, such countries will have to continue to rely on developed country sources for technical grade pesticides and raw materials during the foreseeable future. However, there are strong indications that most developing countries are extremely anxious to promote the establishment of local formulation facilities. In determining the feasibility of establishing such facilities, however, a number of important questions must be thoroughly studied, such as

- (1) choice of products for local use,
- (2) estimated extent of use of each product,
- (3) cost of local formulation vs. importation of finished product,
- (4) local availability of raw materials,
- (5) packaging requirements,
- (6) labeling requirements,
- (7) storage requirements,
- (8) basic laboratory facilities and official regulations to control quality,
- (9) distribution within the country,
- (10) technical advice to formulators, distributors and users,
- (11) application methods, and
- (12) general training requirements in the efficient and safe use of pesticides, etc.

The preliminary survey in use trends and future requirements conducted among developing countries has yielded some valuable information which, in a general way, can be summarized as follows:

1. Information on pesticide consumption, import and local production is not readily available in all countries.
2. More time and some assistance are needed to allow additional countries to generate the necessary information by which their needs can be evaluated.
3. The rate of expansion in the use of pesticides for 1971 through 1973 was considerably higher than had been thought to be the case.
4. The estimates indicate a continuing increase in the rate of use over the next three year period, but at a slightly reduced rate, which is apparently due to generally higher costs and foreign exchange problems, rather than reduced requirements.
5. There is obviously an urgent need to have comparable data from industrial countries and countries employing sophisticated agricultural methods, as consumption in these countries will have an over-riding effect on world availability and demand.

In selecting compounds for local use, a dilemma is being faced by several developing countries over the use of certain persistent organochlorine compounds. In some countries such compounds are being banned, or their use is restricted, because of action in other regions and because of adverse publicity. While recognizing that persistent pesticides should be used under stricter controls and should be eventually substituted by less persistent materials, it appears that, wherever possible, the decision should be based on technical grounds, with full recognition of the consequences of prematurely introducing substitutes which can be more hazardous for use by inadequately informed and trained farmers and, which, as a rule, are most costly. Furthermore, persistence of residues is normally shorter in tropical areas, where most developing countries are located, which would tend to reduce to a certain extent the importance of this normally undesirable property. It should be noted that in 1974 organochlorine insecticides accounted for about 49% of all insecticides used in developing countries, whereas organophosphorous products averaged about 31% and carbamates about 16%. Although use trends demonstrate a gradual increase in all three groups of compounds, the extent of use of organophosphorous and carbamate products is increasing at a consistently and significantly faster rate than the more persistent organochlorines.

The Role of Legislation on Pesticide Development

Basic pesticide legislation and official control procedures at the national level have been identified as an essential first step in promoting the safe and effective use of pesticides. In this regard, the need for uniformity of pesticide legislation and of approaches to problems associated with the registration of pesticides, and the establishment of licensing schemes have been stressed, both by government officials and industry. Furthermore, the need for standard requirements in regard to the licensing of local pesticide formulation plants, especially from the point of view of environmental safeguards and worker safety, has also been pointed out.

Many countries have developed or are currently developing legislation in this regard. However, proliferation of uncoordinated national restrictions and pesticide registration requirements, and hence availability and use, have led to requests for action at regional/global level to bring about greater uniformity as essential to reducing further increases in the cost of developmental research on and

consequently cost of pesticides. Furthermore, the increasing number and diversity of regulatory requirements within and between countries is greatly slowing the introduction of new pesticides originating out of industrial research programs, and preventing most non-industrial discoveries from finding a means to reach the market. This would appear to justify a major study on methods of bringing about some international agreement on regulatory standards and procedures in order to save both time and expense, and allow a number of potentially very useful products to become available for special uses.

In this regard, FAO plans on convening an intergovernmental meeting in 1977 for the purpose of standardizing, where possible, registration requirements internationally. Meanwhile, FAO guidelines on registration requirements have been used by a number of countries as a basis for establishing such requirements.

It is estimated that more than 40 developing countries either have no specific pesticide legislation or if they do, individual schemes are inadequate. This should be seen in conjunction with evidence that unsatisfactory and often misleading labeling of some pesticides, especially those offered by local formulators, re-packers and persons who dispense materials from bulk containers, is known to be a problem in many of these countries. While most major manufacturers endeavor to label their products carefully, there are often serious deficiencies in the precautions, limitations and directions. A need therefore exists for more detailed and more specific directions and training and for an appropriately strong law to control labeling.

Legislation, however, cannot be effective until both sufficiently trained personnel can be recruited to enforce regulations, and technical facilities are established to test samples collected by inspectors. In this regard, the difficulty in providing adequate inspection services has been widely recognized.

To ensure the required quality and stability, adequate and acceptable specifications should be adopted and purchasing agencies should buy only products meeting specifications, such as those published by FAO for products used in agriculture, and by WHO for those used in public health. Regulatory authorities should legislate for similar specifications to protect not only users, but also competitive manufacturers who are prepared to produce satisfactory, stable formulations. Better storage should be developed wherever possible, but, in cases where products cannot retain full potency and physical condition for a reasonable period, at temperatures normally encountered in the countries concerned, such products should be prohibited.

It is generally agreed that official control should be vested in Ministries of Agriculture in order to integrate the legislation with extension and development work. However, it is essential that there should be close coordination and cooperation among Ministries of Agriculture, Health, Commerce and Industry and Trade at the local, national and regional levels.

FAO Program

As mentioned earlier, the importance of pests as a major limiting factor in increasing food production and availability was emphasized by the World Food Conference in 1974 through Resolution X on "Pesticides." This resolution indicated the important place of pesticides in food production, the need for increased use of non-pesticide control measures and the necessity for protection of the environment, and asked FAO, in consultation with other agencies, to initiate the required follow-up action and develop the necessary methods of coordination. FAO called on *ad hoc* Government Consultation in Rome, from 7 to 11 April 1975, to examine the needs in various areas and discuss means of coordination and implementation. The Consultation adopted fourteen sets of recommendations in specific areas involved in protection against pests. Some of them refer to pesticide development. In this connection, it might be useful to review briefly some of the more important conclusions, including requests to FAO to initiate certain new programs mainly designed to assist developing countries to obtain suitable products.

(1) *Pesticide supply demand information*

The *ad hoc* Consultation recommended that FAO, in collaboration with WHO, UNIDO and the pesticide industry, to establish a continuing information system on supply/demand projections for pesticides for a period of 5 to 10 years ahead, and act as a clearing house to help prevent future supply problems for agricultural and public health pesticides. A beginning has already been made in

this regard with the implementation of the first survey mentioned earlier. Future activities in this area will include a program to attempt to determine specific causes and approximate extent of major food losses and define possible remedial measures.

(2) *Registration of pesticides*

A recommendation was made, and has since been approved for implementation in 1977, that FAO, in collaboration with WHO, call on International Consultation to analyze and discuss the basis for harmonizing the requirements for registration of pesticides in different countries. Governmental officials, international organizations, scientific societies, representatives of the pesticide industry, and other interested parties will be encouraged to attend and participate. A preliminary meeting of experts will be convened, prior to the international consultation, to determine the general basis for registration in member nations and to define major points of similarity and of differences with regard to chemical, biological, toxicological, environmental, residue and analytical requirements for pesticides. This will be followed by an attempt to draw up guidelines for acceptance by governments and industry, as a basis for national pesticide registration. Furthermore, the organization and procedures by which petitions for registration are handled, and which are known occasionally to represent an additional limiting factor, may also receive some attention. Thus, while in one country registrations may be processed by a limited number of ministries and bureaus, in another country a whole array of agencies may be involved in a registration process, with the attendant delays and expense that such complexity fosters. It is felt that it would be desirable to the extent possible in keeping with the sovereignty and singular needs of individual nations to achieve a degree of international uniformity in some of these aspects of pesticide registration.

(3) *Development of target-specific pesticides which are not viable for commercial investment*

Interest in integrated pest management has caused entomologists to call for target-specific pesticides which could have the greatest possible impact on target species while at the same time causing minimum effect on other species and the environment. This has led not only to greater interest in developing highly specific insecticides, but also in isolating natural compounds which can be used to manipulate the insect population.

One of the biggest factors which creates difficulty in the development of any such new pesticides is the rapidly increasing research costs required to develop a new product to the market stage. Furthermore, the fact that the development time from discovery to marketing has more than doubled in little more than a decade, to an average time of about ten years, has left a rather short period of patent protection, that does not give a very great incentive for such a large research investment. Besides the research cost, another problem in developing new compounds is the basic cost of manufacture. In the first place, the new discoveries are nearly always more complex molecules than those discovered earlier, and thus are much more expensive to manufacture, as they usually require more steps in their synthesis. This cost is further increased due to the much greater expense for new plant facilities and the greater complexity of plant requirements resulting from more complex synthesis.

Unfortunately, the registration requirements, time schedule and other development costs are essentially the same for narrow-spectrum compounds, with a limited market, and those with a broad-spectrum of activity and wide market potential. Therefore, these specialty compounds would normally require either market acceptance at a greatly increased price, or a much longer commercial life to recover initial investment, before they could become commercially viable. Lack of alternative markets, in case of obsolescence due to new competing materials, build-up of resistance, or price competition changes, and other factors, make such highly-specific compounds a doubtful commercial venture, by comparison with broad-spectrum compounds.

Therefore, if these highly important compounds, for limited markets and specialized uses, are to be developed in the future, it is obvious that some type of international programme will be needed to assist in their development and registration. For example, the World Health Organization has for some time maintained, in collaboration with industrial and private laboratories, a scheme for the evaluation and development of insecticides needed in public health programmes.

It would appear that an international programme for the agricultural sector should be explored. This would require a network of cooperating laboratories and institutions which were capable of conducting all needed biological and chemical evaluations necessary to fulfill registration requirements. This would be a large and expensive undertaking and would require detailed planning and elaboration before it could be launched.

Since any materials would either have originated from private companies or would need to be licensed for sale by the industrial sector, agreement procedures would need to be carefully developed. This might be accomplished through an international trust fund which would be partly reimbursed through licenses and other income from compounds which become commercially successful.

Finally, the Consultation having considered the need for target-specific insecticides and such other pesticides as may be required for integrated pest management; and

Recognizing the many difficulties involved and the lack of incentive for chemical industry to invest adequate time, effort and money in the necessary research and development;

Considered that an international programme offered the only hope of assisting in their adequate development and registration; and

Recommended that a special *ad hoc* meeting be organized to fully explore all the problems and potentials for establishing a workable and useful system for this purpose; and

That pesticide manufacturers be asked to create a task force of their own to examine this question, in close collaboration with FAO, WHO and other interested parties.

(4) *Investment required for adequate pesticide formulation production in developing countries.*

The Consultation was unanimous in recommending that formulation units for pesticides should be set up in as many developing countries as possible, and urged that feasibility studies on this be undertaken by appropriate organizations. It was also important that training centres, preferably regional, be set up for operators/technicians, and that the courses given there include formulation and analytical techniques. It further recommended that regional cooperative projects should be adopted wherever the market in any one country does not justify production for that country's needs only, and where such a solution is feasible, and that UNDP, UNIDO, FAO and WHO should evaluate such projects jointly with the regional economic commissions.

This is a brief outline of the envisaged international activities relating to pesticide development and needs in developing countries.

Although there are at present several problems which are interfering with the rapid changes in research for and development of new chemicals which can more closely meet current and future plant protection requirements, awareness of the difficulties involved is growing and initiative now under way should help resolve some of these problems and accelerate progress. Furthermore, it appears that industry is adjusting its priorities and objectives in the search for new pesticides, and it is logical to assume, indeed expect, that future chemicals will meet more closely the increasingly stricter criteria with regard to safety and the environment and will possess properties more conducive to their use under integrated pest management systems.

Pesticide Development and the Chemical Manufacturer

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ABSTRACT

The pesticide industry is challenged by the pressures of ever-growing requirements for food production contrasted with internal financial and external regulatory constraints. The next decade is likely to see greater selectivity in business — including research — objectives and more determined efforts to strengthen, and make better use of, the science base of crop protection technology. A successful outcome will depend upon commonsense dialogue and cooperation between industry and regulatory authorities and the adoption of realistic attitudes towards the need for adequate patent protection of industrial property.

Mr. Chairman, Ladies and Gentlemen —

I offer you my contribution to the opening stages of this XVth International Congress with some trepidation but also in considerable gratitude. The latter is derived quite simply from the opportunity to spend a week in pleasant and stimulating surroundings, making and renewing friendships and recalling that the 12th Congress in London in 1964 was the first major gathering of its kind that I attended after joining ICI.

The reasons for trepidation will also, I fear, become all too obvious. It has nothing to do with jet-lag — indeed, I am assured that on this occasion I arrived about 1½ hours ahead of my own voice — but it has a great deal to do with the depth and comprehensiveness of what has been said at previous meetings of this body, and what has already been contributed by earlier speakers today.

For example, there is no way that I could attempt to give an industrial version of Sir Vincent Wigglesworth's address (1) to the 1964 Congress, although a better understanding of such basic processes as waterproofing, excretion and sensory perception could lead us to altogether more desirable insect control methods. I read Professor Bey-Bienko's Presidential remarks (2) to the Moscow Meeting in 1968 with particular interest, since we tend to clutch keenly at authoritative crop loss estimates in a field of economics that is still in spite of the efforts of Dr. Cramer and others — for an international field of business, all too imprecisely documented. As an organic chemist I was depressed to read his assessment that only 10% of insect species could be classed as pests, although in relation to a total of 1.5M species this still presents a sizeable challenge. Other estimates refer to 850,000 total species and around 10,000 pests; but the point is still made, and was placed in context by Prof. Southwood's address on Friday.

I fear, too, that the previous speakers in this Congress have already very expertly set in front of you most of the major worries of pesticide manufacturers at the present time.

Professor Southwood has described the armoury of pesticides as a resource to be husbanded by intelligent management, and I would think that anyone looking at the future of, let us say, new cotton insecticides must feel in sympathy with this, whilst recognizing that there may be conflicting factors — the grower has a one-season time horizon, and (as I shall mention later) the armoury is still being renewed with sharper weapons.

Dr. Djerassi has commented upon the investment decision problems facing the pesticide manufacturer, and their likely ultimate consequences for the grower-drawing distinctions on

geographical and cropping basis. I shall also turn with some agreement to this point although it does not necessarily look exactly the same from outside the USA. I was particularly interested in the point, that he only touched upon, relating to actual commercial or semi-commercial support between government and industry.

Dr. Adams also has reviewed the problems of investment decision and harmonization of regulations, and I am grateful to him for the remarks he made about industry's cooperation in technology transfer. I shall return to this point also later in my talk.

I hope, then that you will forgive some unavoidable repetition in what I now have to say: I justify it specifically on grounds of the importance to us all – not just the chemical manufacturer – of the undoubted, all too frequently obvious, and almost certainly worsening world food problem.

With a world population over 4,000 million, and expected to approach 7,000 million by A.D. 2000, we face a rate of increase of around 200,000 mouths per day. (That will be around 5,000, or about two entomological congresses, by the time I sit down).

According to FAO, 10-15% (over 400 M people) are under-nourished in calorie terms, quite apart from those that suffer protein or vitamin deficiencies, and yet it is estimated that overall we still lose around 1/3 of our potential food supplies to pests and weeds, although in areas of high pesticide usage such as Japan, Western Europe and USA the loss levels may be somewhat lower. Dr. Aders has reviewed this aspect of pesticide usage, and it would be presumptuous of me to comment further.

The problem is clearly not only one of loss to pest, disease or weed. Many other factors such as conflict with social habits and inadequacy of food distribution chains are also involved; indeed, where these involve educational or training performances it is important for the pesticide manufacturer to associate himself with the local agricultural extension organization to ensure safe and effective use of suitable products.

However, the aspects that I particularly want to discuss are the need, opportunity, and likelihood of the combined existence of a healthy and forward looking agricultural industry, with the heavy and risky investment of money in physical resources and peoples skills which that implies. If I examine this largely from an R&D point of view, it is partly because this has been my own background, but more because I believe that the future contribution of the industry to agricultural technology will continue to depend upon its willingness to put together R&D teams that are interdisciplinary, international and highly expensive in a changing area where the rules of the game sometimes seem apt to change overnight.

I will not dwell over long on the question of continued opportunity for innovation; suffice it to say that this is probably the key question in every long term planning session in every corporation engaged in this field of business. It must be added that a superficial look at the number of major new product introductions in recent years is discouraging – Dr. Goring has presented estimations:

1931 – 40	1
1941 – 50	9
1951 – 60	18
1961 – 70	19
1971 – 1974	3

However, I believe that a technical analysis of opportunities shows that there continues to be a need for safer, more effective, and/or more specific materials in existing uses, and that there are fields – such as nematicides and plant growth regulators and that we have hardly begun to explore. Crop protection technology is still relatively primitive, and the recent emergence of new generation insecticides only underlines the scope for further advance.

While we are thinking about the increase of food supplies, it is also worth remembering the very low percentage component of total crop production energy inputs that is accounted for by pesticides; for example, figures ranging from 0.9% (UK overall average) to 1.4% (UK potatoes) and 1.9% (US maize) are quoted by M.B. Green in a particularly interesting recent article in Chemistry and Industry, carrying the subtitle “how long can we go on eating oil?”. As some indication of the overall energy equation in agriculture, the British Agricultural worker feeds himself and 47 other people from one day's work pm 0.78 hectares of land but with an energy output/input ratio of only 0.4. Looking at this a different way, the African bushman achieves about 20 times as much output for a given input of energy, but requires 1,300 times as much cultivated land to do so.

The continued ability to engage in agrochemical business is based upon shareholders' money and therefore shareholders' confidence; the shareholder in our business may be the man in the street, or the Institutional investor, or (more often) it is in effect the corporation of which the agrochemical division is a part. The principal is the same. In either case the business must meet its outgoings, including direct cost of product, selling costs and R&D expenditure and must over a period finance its own capital investment, and must be able to pay a regular dividend. The latter commonly takes the form of cash flow to the corporation; the net cash flow must normally be positive, or inward, or the organization's investment funds will be switched into other fields — pharmaceuticals, dyestuhs, plastics, etc. — that may offer higher return and might well carry lower risk. The manufacturers have no obligation to go on making pesticides, and no one should expect them to do so if it ceases to be sufficiently rewarding.

I am sure that it is well understood that the pesticide manufacturer must operate within these financial constraints, and that on this basis, there is current cause for concern; early symptoms have been the gradual withdrawal, or retrenchment, of several agrochemical manufacturers (there are still around 100 left) and the fear on the part of specialized segments of agriculture that their own crop protection requirements might in future not be met. I should like to examine the way in which these situations arise, in the light of the external constraints placed upon the industry, since these reflect directly, and in financial terms, upon the internal ability of the organization to survive profitably.

In exploring this theme, I acknowledge my debt to others who have been this way before me; especially Dr. Goring, of Dow (*Brighton 1975*), (4) Dr. Green of ICI (*Atlanta Weed Science 1973*), (5) and Dr. Knusli (*Helsinki 1974*) (6).

Evolution of Ag Chem

The innovative process that leads from the research worker's bench to useful application by the farmer is a complex one, and is illustrated by Fig. (1). The slide illustrates this — Dr. Gysin has exemplified it far better than I could. There are essentially three streams flowing side by side. The first of these is the discovery, in the laboratory, of a succession of chemicals or techniques that produce effects that are likely to be desirable, and the second, the evaluation of a selection of these

ESTIMATE OF DEVELOPMENT COSTS OF A PESTICIDE
BREAKDOWN OF ESTIMATES

	M.B.GREEN %	ERNST & ERNST %
SYNTHESIS & SCREENING	29 · 9	29 · 7
FIELD TESTING & EVALUATION	30 · 7	31 · 7
TOXICOLOGY & ENVIRONMENT	14 · 8	14 · 6
FORMULATION & PROCESS	18 · 2	17 · 9
REGISTRATION & PATENT	6 · 4	6 · 1

essentially in a cost/benefit sense. An indication of the relative cost contribution of different stages of R&D is shown in Fig. (2).

The technical approach to these activities has perhaps changed surprisingly little during the last ten years, but there is no doubt that a much more rigorous assessment is now being made of the financial viability of our target effects, which is itself dependent upon their long-term utility to the farmer. It has been suggested, for example, that the discovery process should not deliberately be aimed at targets for which a market of at least \$10M cannot be envisaged. I doubt whether any organization would wish to observe so rigid a constraint, but it is quite clear that so-called minor corps and minor uses must be disappearing from our repertoire of primary screening targets particularly if the candidate product is not already in, or under test for, a major outlet; where there are deficiencies in available treatments, these will in such cases have to be met mainly by the relatively ad hoc response of mixtures or formulation improvement, unless options such as the IR-4 processes in this country gather momentum successfully. We have recently renewed our efforts at target definition in my own organization; it would be premature and therefore indiscreet, to discuss the outcome, but all the signs bear out what I have just said.

NUMBER OF COMPOUNDS PASSING THROUGH EACH R & D STAGE
PER COMMERCIAL PRODUCT

(Field 1964 ,von Rumker 1970, Ernst & Ernst 1971, Johnson & Blair 1972)

Activity	1956	1964	1967	1969	1970	1972
Synthesis & initial bio -screen	1800	3600	5500	5040	8000	10000
Advanced screening	60	36	NA	126	80	NA
Field evaluation	6	4	NA	9	4	NA
Development	2	2	NA	2	2	NA
Sales	1	1	1	1	1	1

There is equally no doubt that the most important success of our exploratory research – some 35% of total R&D effort – would be to achieve the next discontinuity in crop protection technology – and this appears by definition to be unforecastable and largely unplannable. To digress the greatest contribution will be derived from the development of first rate entities with responsive management and an organization developed to aid creativity.

In a situation where the transition from test-tube to farmer's spray may take seven or eight years, and cost \$5M-\$10M, patent protection for a reasonable proportion of subsequent sales life is also vital. It is a matter of immediate concern, and possible longer-term damage to crop protection science and technology, that actual or proposed legislation in various parts of the world is now tending to reduce patent protection at a time when the industry's costs are rising so steeply. The reasons are understandable, but I believe that this is a situation where harmful long-term side effects on industry strategy can be accurately predicted and should not be ignored.

I mention crop protection science, and will return this briefly in a few moments; at this point I would simply like to note that our activities are still to a regrettable degree independent of science and reliant upon empiricism. I am sure we have all discussed with our colleagues the hazards, and potential benefits, or trying to break away from this situation.

The evaluation process may typically receive around 100 candidates (from 10,000 originally screened) warranting field investigation of progressively increasing severity until perhaps only one remains to place on the dealers' shelves (Fig. (3)).

The importance of speed and accuracy in defining potential value in the real agricultural situation, and in some places the increasing difficulty of arranging trial programs with cooperators, has led to the setting up of international biological research centres. Apart from once again stressing the need for a truly international catchment as the basis for a viable industry, I would like to remark upon two incidental aspects of research co-operation; in the first place, I believe that there are opportunities at establishments such as these field centres for reciprocal assistance in in field experimentation between industry and workers in universities, land grant colleges, extension services, etc. Secondly, the need for economical managerial control of such networks through effective information handling systems is so universal that, like toxicological and environmental techniques it should probably be the subject of more open exchange of experience between industrial practitioners so that we all pay the minimum necessary tax to the God of Communication.

The third mainstream of development activity is the assurance of acceptable toxicological and environmental standards for everyone directly or indirectly involved in the use of agricultural chemicals. It is here especially that the world in which industry lives has changed considerably during the last ten years, and the situation has been very clearly described for us by Dr. Whittemore and Dr. Cramner.

I would certainly not quarrel with the direction of the change, nor in a general sense with its extent; however, as a comment upon some of its most recent manifestations I make a strong plea for preeminence in the regulatory process of technical understanding extended by realism and common sense and confounded by a minimum of legalistic process. (I draw encouragement from Dr. Whittemore's remarks in this respect). To achieve this, complete openness in a prerequisite on both sides coupled with a genuine belief that the purpose of the regulatory process is to ensure that agriculture continues to receive the supply of safe and effective products that it needs.

The impact of the work properly required by regulatory bodies on the industry's time scale and costs is of course very significant, and activities such as long-term feeding studies, soil metabolism and ecological research are generally quantum level, at least in some areas, unless selectivity of targetting is pursued much more sternly than hitherto. Dr. Djerassi has already referred to this, especially in the context of new types of product. Secondly, the problem is aggravated by the size of the bill involved. For example, total toxicological charges within a major crop protection R&D budget can exceed \$2M annually, with a similar cost for environmental work in addition; all of this is risk money, with no assurance that a marketable product will ultimately emerge.

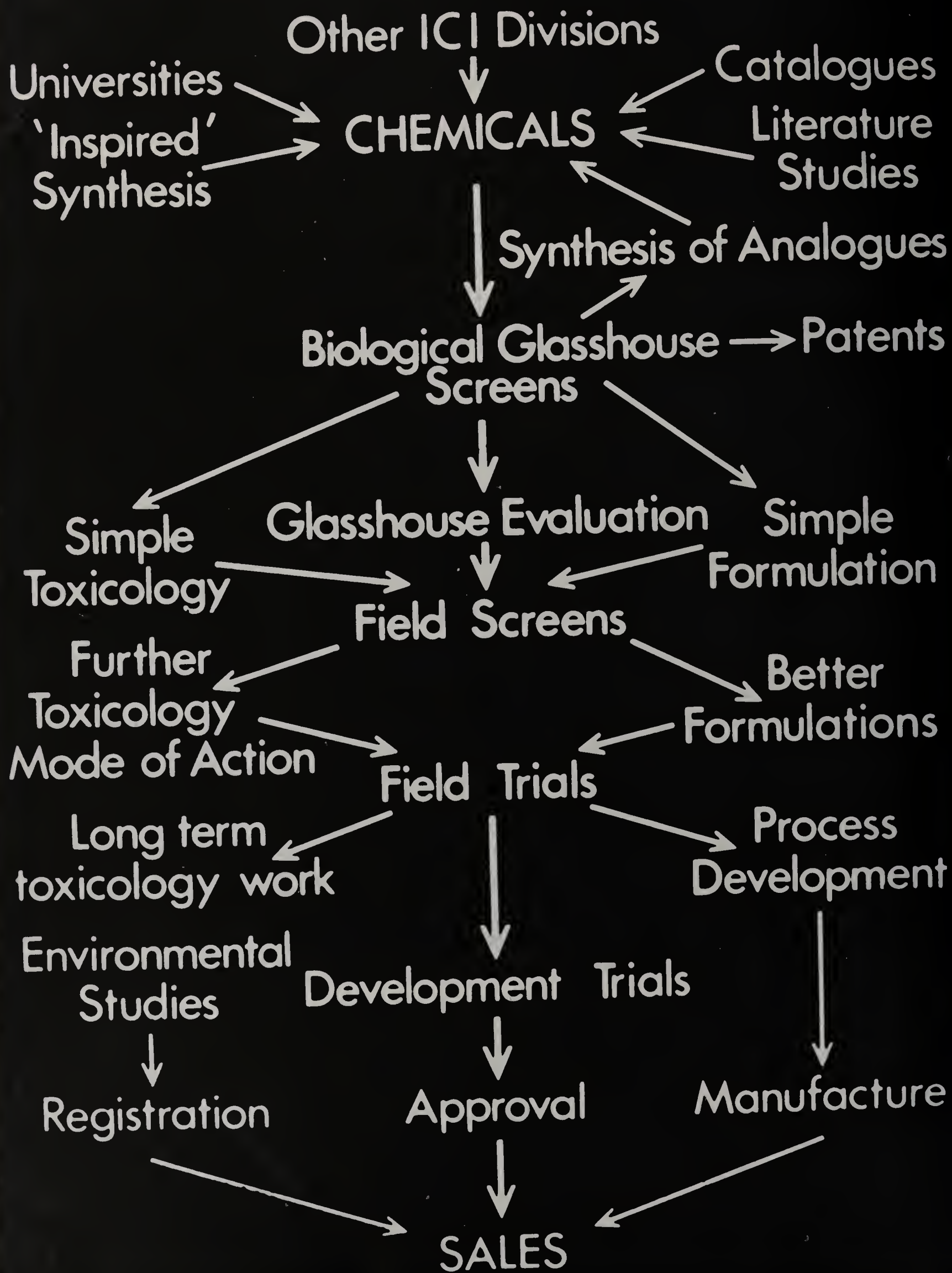
In conclusion of this first part of my talk, I would now like to use a simple cash flow diagram (Fig. (4)) to sum up the decisions facing the pesticide manufacturer from the point at which a candidate product has been identified.

We find ourselves at the beginning of a long and slippery slope, with money flowing out "now" for possible reward "then" the length and depth of which will be materially affected by the quality of decision —

- (a) Which compound to select from a family — chemistry & possible m/f technology.
- (b) What uses/markets — how many do we look at at once?
- (c) What are the early environmental signals: design of environmental work.
- (d) What about early toxicology?
- (e) What formulation — the choice is often later than we would like in relation to (c) and (d), owing to the effect of formulation on field performance.
- (f) What is the competition doing?

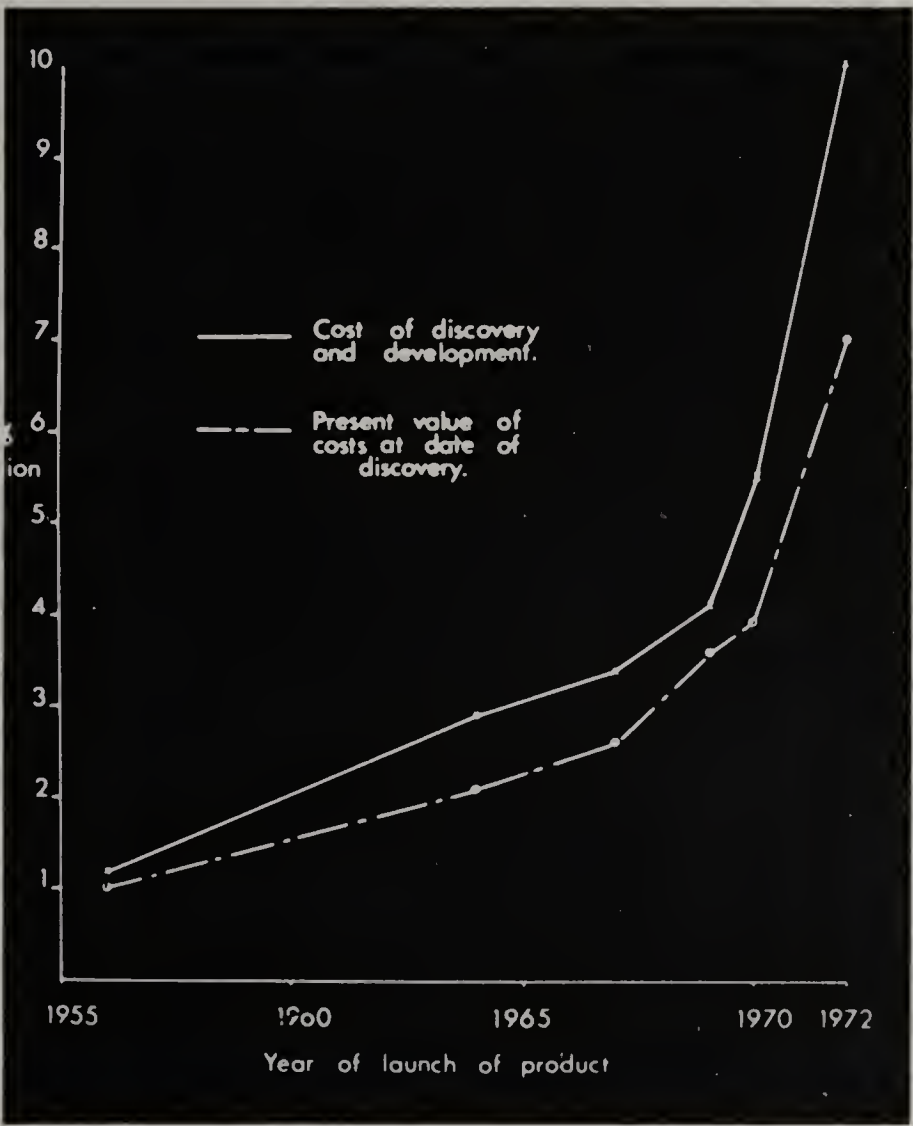
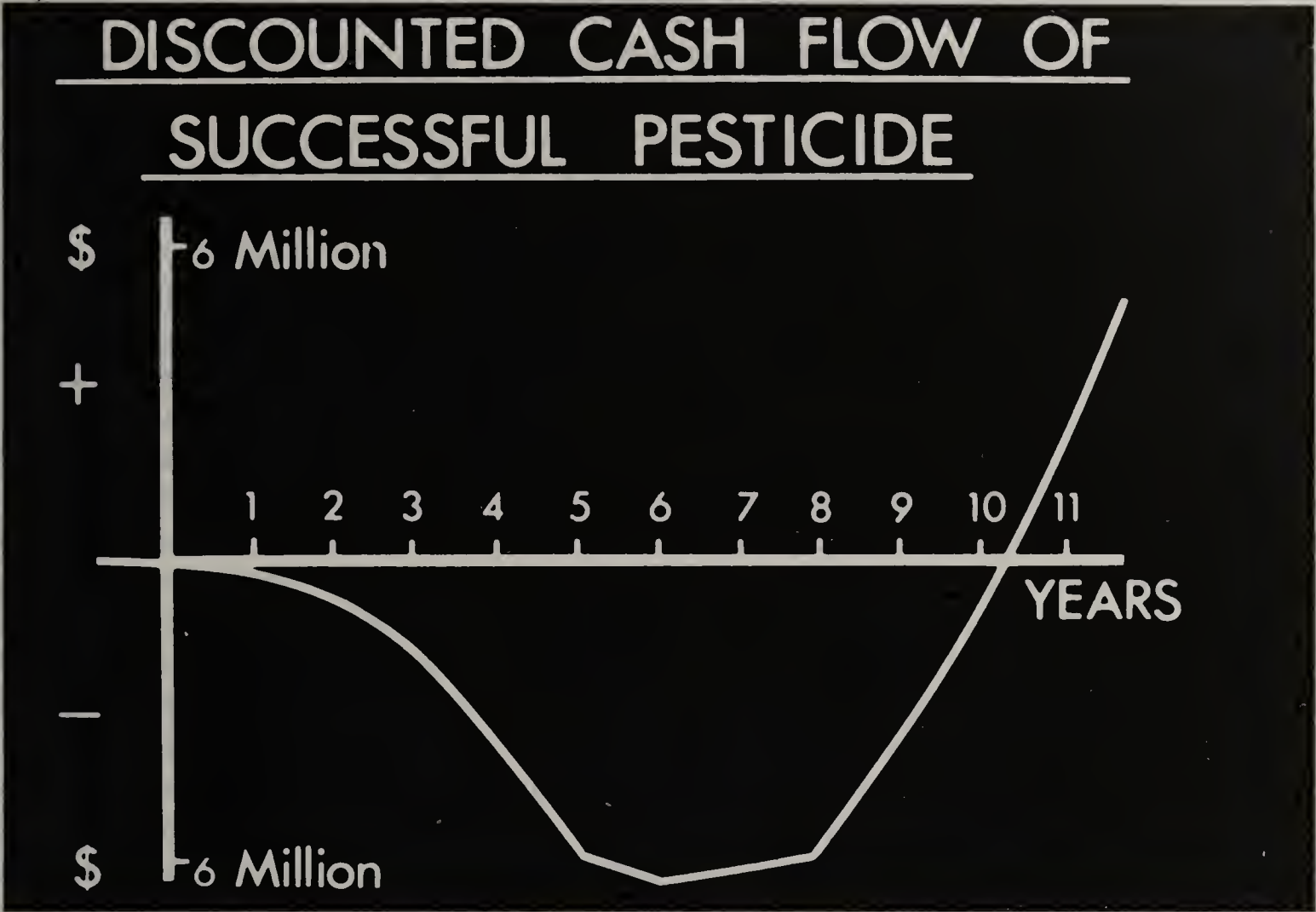
It is commonly not until around year ten after discovery that the annual incomings and outgoings first balance on an annual basis; during this time some \$6M to \$7M may have been spent on development alone, and with a further \$10M to \$20M required for even small scale production facilities the magnitude of the investment risk is clear. Fig. (5) shows how R&D costs have grown over recent years. Even at this stage, it is not uncommon for a growth project to return to a negative cash flow when considerable investment in extra capacity is required. Nevertheless, increased scale of

Discovery and Development of a new Pesticide



manufacture can normally be a major factor in increasing efficiency of production; this is not generally achieved through a multiplicity of small plants, a fact to which due weight has to be given when considering proposals for technology transfer – for example, under FAO/ICP auspices.

In this context the annual meetings involving the developing countries FAO and industry, organized by Dr. Adams are very important.



So much for the problems and external constraints; they are real, and potentially damaging, but I would not like to finish without stressing that I nevertheless see a hopeful future for the pesticide industry, or at least for that part of it that is both skillful and lucky in the use of its R&D resources. To achieve this future will undoubtedly require change in which there will be a number of elements.

In the first place, I have suggested one or two areas in which more effective collaboration could probably be achieved between members of the industry. These include toxicological protocol, environmental techniques, analytical methods and information handling procedures. In all of these, and in consultation on patent matters, progress is being made but sometimes only slowly and in the face of suspicion.

It is in my opinion even more important to expand the science base upon which the future of crop protection depends. Recent discoveries — latest generation of pyrethroids, (about which surprisingly little is being heard this week) and materials interfering with chitin metabolism for example give real hope for the discovery of still newer pesticides of previously unknown levels of activity and selectivity. I think it is increasingly unlikely that such discoveries will be made economically by our traditional reliance on chance; particularly interesting reviews on this subject were presented at the 1975 Brighton Conference by Dr. Corbett (8) and by Dr. Graham Bryce (9).

However, it is out of the question that industry can within itself play a major part in advancing then enabling sciences. I therefore look for increasing help from workers in fields such as insect biochemistry in academic and other establishments where truly basic research is properly carried out, and progressively increasing collaboration between such establishments and the long-term workers in industry who may be best placed to relate new science to technological need or opportunity. Some examples of the kind of thing that will emerge are included in the Chem Week review Pesticides 76, to which I have already referred, under headings such as Behavior Control and Gene Juggling. As a simple illustration of the way this can be done, I would cite the corporately-funded Joint Research Scheme operated by my own Company, in which support is directed to projects of basic scientific importance within or extending fields of technology that are of significance to the operant units.

I believe that a successful future for the industry depends not only upon greater support for, and dependence upon, the basic sciences, but also upon increased awareness of the ecology and agronomy of the total agricultural systems with which we are interacting. The deliberate use of highly selective agents such as aphicides in integrated control programmes, is a relatively simple example; total environmental impact, for example, upon cropping pattern, soil structure and farmer leisure, of reduced cultivation systems based upon contact herbicides is a rather more complex case; and the interrelationship of chemical manufacturer and plant breeder is a third. These are all illustrations of the way in which we are becoming pest managers with an increasing — should I say returning? — understanding of total agricultural systems.

Will this ultimately lead the pesticide manufacturer to a closer involvement in the actual process and technology of application? I would prefer to leave this as a rhetorical question at this stage of the morning, but it is not one that can be ignored by the industry — particularly as more active but more expensive materials become available. Problems of placement and timing may in future be crucial, and especially I suspect if the possibilities of plant growth regulation are to be exploited to the full.

In summary, I believe it can be recognized as clearly as ever — and this was being said by Dr. E.F. Edson in his plenary address to the Brighton Conference in 1973 — that there is a great and increasing need for a profitable, scientifically-based and forward-looking agrochemical industry. And that this industry accepts regulation in the interests of the user and consumer and the environment we all share provided that this is applied through a consultative process and with a wise blend of technical expertise, legal constraint and common sense — often called good old-fashioned common sense but, let us hope, not thought to be out of date as a consequence.

There are, I believe, distinct threats to the viability of the industry in the eyes of major companies from which future innovation should originate; this threat is becoming reality in the area of minor crops and minor outlets, although recent or proposed government actions point the way to some alleviation of the problem.

I feel considerable personal concern over the inadequacy of our science base; I hope that we may see increasing commitment of money and effort to fundamental research, perhaps especially in the fields of insect biochemistry and physiology, and that in the process there will be steady increase in understanding and respect between industrial and academic scientists. I am sure that there are fields of entomological science and technology in which we could be of more help to each other.

It is with this particularly in mind that I should like to conclude by reiterating my own pleasure and gratitude at being here at the XVth International Congress. The programme and the list of contributors seem, as we start our meetings, to underline the health of scientific and technological collaboration between entomologists in industry and in University of Government employment; this was particularly evident in the range of topics proposed for Congress and Section symposia.

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**Section 13: Pesticide Development, Management, and Regulation;
and Section 4: Toxicology**

PESTICIDE RESISTANCE I

Organizer: A.W.A. BROWN (USA)

Moderator: F.W. WHITTEMORE (USA)

Pesticide Resistance as an Evolutionary Phenomenon

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ABSTRACT

Since the last survey of resistance in 1967, the number of species of insects and acarines in which resistant strains have evolved has increased by 62.5% to a total of 364. Of these, 225 are of agricultural importance and 139 of medical/veterinary importance. Simultaneously, significant increases have occurred in the geographic distribution of resistant strains and in the spectrum of pesticides which can be tolerated, so that the phenomenon of resistance is asserting itself as the greatest challenge to effective control of many important pests.

The relative dearth in the development of new chemicals, and recent demonstrations of the ability of populations to evolve resistance to pyrethroids and development inhibitors, focus greater emphasis on the necessity for incorporating resistance-avoiding or resistance-delaying considerations in pest management systems.

To that end, the authors present a survey of the present status of resistance in insects and acarines and discuss the genetic, biological and operational parameters which influence the selection and evolution of this phenomenon in field populations.

Despite its grave economic consequences, the phenomenon of resistance to pesticides has received surprisingly little attention from evolutionary biologists. Yet it presents excellent opportunities, not only for the study of fundamental aspects of micro-evolution in man-altered environments, but also for the formulation of strategies for countering the course of this phenomenon for the benefit of mankind.

Resistance of insects to insecticides has a history of nearly 70 years, but its greatest increase and its strongest impact have occurred during the last 30 years following the discovery and extensive use of synthetic organic insecticides and acaricides. Resistance in plant pathogens is of more recent origin, the first case having been detected 36 years ago (Farkas and Aman 1940). However, numerous cases of resistance in these organisms have been reported during the last decade coincident with the introduction of systemic fungicides (Georgopoulos and Zaracovitis 1967, Dekker 1972, Ogawa et al. 1976). Resistance in noxious weeds is still more recent (Ryan 1970, Radosevich and Appleby 1973), and so far has been detected only at low levels in species associated with crops which have been consistently protected with herbicides. Resistance of nematodes toward soil fumigants has not yet been detected; however, the recent introduction of systemic nematocides raises strong possibilities of resistance in this group as well.

Considerable advances have been made in the study of the biochemical/physiological mechanisms of resistance, especially in arthropods. Progress involves the biochemical characteristics of specific defense mechanisms (reviews by Motoyama and Dauterman 1974, Hodgson et al. 1974, Terriere and Yu 1974, Perry and Agosin 1975), their genetics (reviews by Georghiou 1969, Plapp 1976), interactions (Georghiou 1971, Sawicki 1974), and their quantitative contribution to resistance. But the evolution and dynamics of resistance in field populations are inadequately known (review by Georghiou 1972b), and relatively little has been contributed in terms of unique schemes of population management aimed specifically at avoiding or reversing the process of resistance development while achieving satisfactory pest control. This paper reviews briefly the present status of

resistance in arthropods and emphasizes the known and presumptive parameters which influence its evolution in field populations.

Present Status

Quantitative, Qualitative and Geographic Aspects

The number of species of insects and acarines in which resistant strains have been reported since the first occurrence of resistance (in *Aspidiotus perniciosus* toward lime sulfur) in 1908 (Melander 1914) are given in Table 1. The increase in recent decades has been almost linear, the numbers of species having risen by the end of 1975 to a total of 364. This latest tabulation has been facilitated by FAO through a 1974-75 world-wide survey of resistance in agricultural pests. Included in Table 1 are also the cases of resistance in insects of medical importance which have been recently catalogued by WHO (1976). Although an attempt was made to also include all cases reported in the literature, some may inadvertently have been missed. It is therefore not unlikely that the actual number is greater than the one given above.¹

Table 1.—Number of species of insects and mites in which resistance to one or more chemicals has been documented.¹

Year	Species
1908	1
1928	5
1938	7
1948	14
1954	25
1957	76
1960	137
1963	157
1965	185
1967	224
1975	305 ²
	(+ 59 unconfirmed)

¹ Data from various sources.

² This Report; see Tables 3 and 4 for species involved.

The distribution of cases of resistance among different Orders, and the types of chemical groups involved, are indicated in Table 2. Of the 364 cases on record, 139 involve species of medical and veterinary importance and 225 are species of agricultural importance, including forest and stored product pests. Among the various Orders, most cases are found in the Diptera, due obviously to the large number of species of resistant Culicidae, followed by approximately equal numbers of resistant species in the Coleoptera, Hemiptera and Lepidoptera. Qualitative as well as quantitative impressions of the evolution of resistance in recent years may be obtained by comparing the data in Table 2 with those in Table 7-1 in Brown (1971). The latter includes records mainly through 1967, thus the differences may be assumed to represent cases emerging during the 8 year period 1967-75. In terms of total numbers of species involved, there has been an increase of 140 species (62.5%) of which 20 (16.8% increase) are of medical and 120 (114% increase) of agricultural importance. Among the various Orders, substantial increases have occurred in the Coleoptera (143% increase), Lepidoptera (79%), Acarina (79%), Hemiptera (57%) and Diptera (44%). With regard to the chemical groups concerned, large percentage increases are evident in the organophosphates (172%), DDT (107%), and

¹ The author would greatly appreciate receiving communications from colleagues regarding new cases of resistance.

the carbamate categories. Nearly all cases of carbamate resistance (33) are new. The smallest increase (60.7%) involves the cyclodienes, possibly due to a decrease in the extent of usage of these compounds.

Table 2.—Number of species of Arthropoda with reported cases of resistance to pesticides.

	Pesticide Group					Med.	Agr.	Total
	DDT	Cyclod.	OP	Carb.	Other			
Acarina	21	10	32	6	13	10	33	43
Anoplura	5	3	2			5		5
Coleoptera	26	48	18	7	8		56	56
Dermaptera	1						1	1
Diptera	91	100	40	6	4	110	23	133
Ephemeroptera	2						2	2
Hemipt./Het.	4	12	3			4	10	14
Hemipt./Hom.	10	11	28	4	4		41	41
Hymenoptera	1	1					2	2
Lepidoptera	31	32	22	12	4		52	52
Mallophaga		2				2		2
Orthoptera	3	1	1	1		3		3
Siphonaptera	5	3	1			5		5
Thysanoptera	3	2			2		5	5
	203	225	147	36	35	139	225	364 ¹

¹ Includes 59 species reported on basis of field tests or observations; of these 3 are of medical/veterinary importance and 56 of agricultural importance.

The names of species of acarines and insects in which resistant strains have appeared are arranged taxonomically in Tables 3 and 4, respectively, and distinction is made between records based on field tests or observations (cases marked by +), and those confirmed by laboratory tests (cases marked by *). In addition to conveying the species by species status of resistance, the records also suggest the relative tendency for evolution of resistance in specific families or groups. Attention should be drawn to the increasing appearance of organophosphorus resistance in certain agriculturally important families as the Tetranychidae, Anthomyiidae, Miridae, Aphididae, Cicadellidae, Noctuidae, Phycitidae, and Yponomeutidae (see Table 4).

In considering the status of resistance, emphasis must be placed not only on its numerical occurrence among species, but also on the geographical distribution of resistant populations, the frequency of resistant genes and the number of chemicals which can be tolerated. An outstanding example of nearly ubiquitous resistance is that involving DDT and cyclodienes in *Musca domestica*. Almost universal is also resistance to malathion and lindane in *Tribolium castaneum* (Dyte 1974). In *Culex tarsalis* in California (Gjullin and Isaak 1957), organophosphorus resistance had involved almost the entire agricultural Central Valley within a decade (Fig. 1) (Womeldorf et al. 1972). Similarly, in *Anopheles albimanus*, organophosphorus and carbamate resistance, which appeared in the center of coastal El Salvador in 1969, had encompassed within 5 years most of the Pacific coastal zone of El Salvador, Guatemala, Honduras and Nicaragua (Georghiou 1972a and unpublished data). In malaria control activities, it has recently been estimated by WHO (1976) that the areas where vector resistance is a problem are inhabited by 256 million people, or 29% of the total population of the malarious areas.

Economic Aspects

The impact of resistance should be considered not only in terms of greater costs of pest control due to increased dosages and number of applications, but also in terms of the ecological disruption of pest-beneficial species density relationships, the loss of investment in the development of the

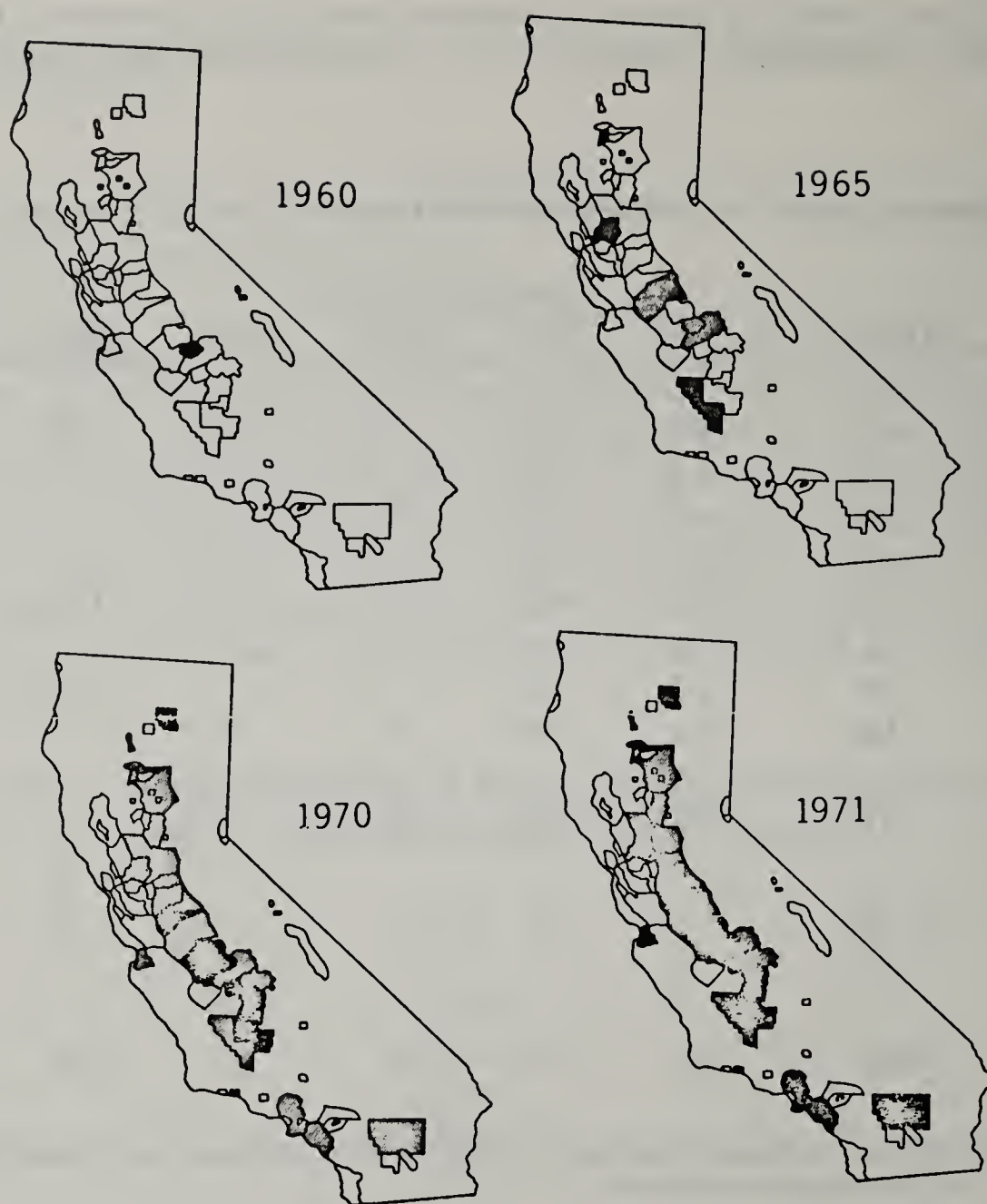


Fig. 1. —The spread of organophosphorus resistance in *Culex tarsalis* (adapted from Womeldorf et al. 1972). Resistance to one or two materials (light shaded areas) and to several materials (dark areas).

pesticides concerned, and socio-economic disruptions in agricultural communities. Disruptive effects in pest control are usually caused by the presence of chemicals unfavorable to the beneficial species, and are accentuated as dosages and rates of application are increased commensurate with the development of resistance in the pest species. Unfortunately, because of density dependence characteristics, beneficial species are less consistently selected for resistance so that to date only 7 species of phytoseiid mites (*Typhlodromus occidentalis*, *T. pyri*, *T. caudiglans*, *Amblyseius fallacis*, *A. chilenensis*, *A. hibisci*, *Phytoseiulus persimilis*), and one coccinellid (*Coleomegilla maculata*), have evolved resistant field strains (reviews by Georgiou 1972b, Croft and Brown 1975, Croft 1976).

If a monetary value is to be attached to the more tangible losses, the following rough estimates may be of interest:

a. Increased dosages and numbers of application: The cost of insecticides applied in the U.S. in 1972 (latest figure cited by NAS [1975]) was \$166 million. If at least 50% of these applications are required because of resistance, this cost alone would amount to \$83 million annually.

b. Loss of pesticide development investment: The cost of developing an agricultural chemical was estimated at \$1.2 million in 1956, \$4.1 million in 1969 (Hunter 1974), and \$13 million in 1975 (W. Mullison, in Lewert 1976). Considering that at least 57 commercial insecticides and acaricides have been affected by resistance (including DDT, most cyclodienes and many organophosphates and carbamates), and that cross resistance from other insecticides often affects the field effectiveness of a new product, it may be assumed that a number of compounds have not returned the investment involved in their development. Certain cyclodienes, the carbamate mexacarbate, and a number of acaricides may be examples. No estimates are available of these losses but it may be safely assumed that they are substantial.

Table 3.—Cases of resistance to pesticides in Arachnida.¹

Vet. Med.	Agr.	DDT	Cyclod.	OP	Carb.	Sulfonate	Sulfone	Other
ACARINA								
	Acaridae							
	<i>Acarus siro</i>		*					
	Dermanyssidae							
*	<i>Ornithonyssus sylviarum</i>			*				
	Eriophyidae							
	<i>Aculus cornutus</i>			*				
*	<i>A. fockeyi</i>			+				
*	<i>A. malivagran</i>			+				
*	<i>A. pelekassi</i>	+						
*	<i>Phyllocoptruta oleivora</i>				*			
*	<i>Vasates schlechtendali</i>			*				
	Ixodidae							
	<i>Amblyomma americanum</i>	*	+					
*	<i>A. variegatum</i>		+					
*	<i>Boophilus decoloratus</i>	*	+	*				Sodium arsenite*
*	<i>B. microplus</i>	*	*	*	*			Sodium arsenite*
*	<i>Dermacentor variabilis</i>	*	*					
*	<i>Hyalomma marginatum</i>		*					
*	<i>Rhipicephalus</i>							
	<i>appendiculatus</i>	*	*					
*	<i>R. evertsi</i>	*	*					
*	<i>R. sanguineus</i>	*	*					
	Phytoseiidae							
	<i>Amblyseius fallacis</i>			*	*			
*	<i>A. hybisci</i>			*				
*	<i>Typhlodromus occidentalis</i>			*	*			
*	<i>T. caudiglans</i>	*						

Table 4.—Cases of resistance to pesticides in Insecta.¹

<u>Vet.</u> <u>Med.</u>	<u>Agr.</u>	<u>DDT</u>	<u>Cyclod.</u>	<u>OP</u>	<u>Carb.</u>	<u>Fumigant</u>	<u>Other</u>
ANOPLURA							
*	Haematopinidae <i>Haematopinus eurysternus</i>	*	+	+			
	Linognathidae <i>Linognathus africanus</i>	*	+				
	<i>L. stenopsis</i>	*					
	<i>L. vituli</i>	*					
*	Pediculidae <i>Pediculus humanus</i>	*	*	*			
	COLEOPTERA						
*	Bostrichidae <i>Rhizopertha dominica</i>		*	*		MB*, Phosphine*	
	Buprestidae <i>Diatraea saccharalis</i>		*				
*	Byturidae <i>Byturus tomentosus</i>	+					
*	Carabidae <i>Clivina impressifrons</i>		*				
*	Chrysomelidae <i>Brontispa longissima</i>		+				
	<i>Diabrotica balteata</i>	+	*				
	<i>D. longicornis</i>	+	*				
	<i>D. undecimpunctata</i>		*				

Vet.
Med.

Med.	Agr.	DDT	Cyclod.	OP	Carb.	Fumigant	Other
*	<i>D. virgifera</i>	+	*				
*	<i>Epitrix atomaria</i>	+	+				
*	<i>E. cucumeris</i>	*	+				
*	<i>E. hirtipennis</i>	+	+				
*	<i>E. tuberis</i>	*	*				
*	<i>Galerucella birmanica</i>	+	*				
*	<i>Lema (=Oulema) oryzae</i>	+	*				
*	<i>Leptinotarsa decemlineata</i>	*	*	*			
Coccinellidae							
*	<i>Coleomegila maculata</i>	*	*	*			Rotenone*
*	<i>Epilachna varivestis</i>						
Cucujidae							
*	<i>Oryzaephilus mercator</i>		*	*		EDB*	
*	<i>O. surinamensis</i>		*	*			
Curculionidae							
*	<i>Anthonomus eugeni</i>			+	+		
*	<i>A. grandis</i>	*	*				
*	<i>Bothynoderus punctiventris</i>		*				
*	<i>Ceutorrhynchus assimilis</i>	+	+	+			
*	<i>C. quadridentatus</i>	+	+	+			
*	<i>Cosmopolites sorditus</i>		*				
*	<i>Cylas formicarius</i>	+	+				
*	<i>Eutinobothris brasiliensis</i>		+				
*	<i>Graphognathus leucoloma</i>		*				
*	<i>G. minor</i>		*				
*	<i>G. peregrinus</i>		*				
*	<i>Hypera postica</i>		*				
*	<i>H. variabilis</i>	*	*				
*	<i>Lissorhoptrus oryzaephilus</i>		*				
*	<i>Miccotrogus picrostris</i>	*					
*	<i>Phytonomus variabilis</i>		*				
*	<i>Sitophilus granarius</i>	*	*	*	*	EDB*, MB*, Phosphine*, HCN*	
*	<i>S. oryzae</i>	*	*	*	*		
*	<i>S. zeamais</i>	*	*	*	*		

<u>Vet. Med.</u>	<u>Agr.</u>		<u>DDT</u>	<u>Cyclod.</u>	<u>OP</u>	<u>Carb.</u>	<u>Fumigant</u>	<u>Other</u>
		DIPTERA						
		Agromyzidae						
	*	<i>Liriomyza archiboldi</i>		*				
	*	<i>L. flaveola</i>	+		+			
	*	<i>L. munutiseta</i>			+			
	*	<i>L. munda</i>			+	+		
	*	<i>Phytomyza atricornis</i>		*				
		Anthomyiidae						
	*	<i>Erioischia brassicae</i>		*				
	*	<i>Euxesta notata</i>	*	*				
	*	<i>Hylemya antiqua</i>	+	*	*			
	*	<i>H. brassicae</i>	*	*	*			
	*	<i>H. cilicrura</i>		*				
	*	<i>H. floralis</i>	+	*				
	*	<i>H. florilega</i>		*				
	*	<i>H. platura</i>		*				
*		<i>Ophyra leucostoma</i>	*	*				
		Calliphoridae						
		<i>Chrysomya bezziana</i>		*				
*		<i>C. putoria</i>	*	*	*			
*		<i>Lucilia</i> (=Phaenicia) <i>cuprina</i>	*	*	*	*		
*		<i>Phaenicia sericata</i>	*	*				
*		<i>Protophormia terraenova</i>	*					
		Cecidomyiidae						
	*	<i>Dasyneura pyri</i>			*			
		Ceratopogonidae						
		<i>Culicoides furens</i>		*				
*		<i>Leptoconops kerteszi</i>	*					
*		<i>Chaoborus astictopus</i>	*					
		Chironomidae						
*		<i>Chironomus zealandicus</i>		*				
*		<i>Glyptotendipes paripes</i>		+				

Chloropidae

Hippelates collusor

Culicidae

Aedes aegypti

A. albopictus

A. atropalpus

A. cantator

A. cantans

A. caspius

A. detritus

A. dorsalis

A. fijiensis

A. melanimon

A. nigromaculis

A. polynesiensis

A. pseudoscutellaris

A. sierrensis

A. sollicitans

A. taeniorhynchus

A. togoi

A. triseriatus

A. vexans

A. vittatus

Anopheles aconitus

A. albinus

A. albitarsis

A. annularis

A. aquasalis

A. atroparvus

A. barbirostris

A. coustani

A. crucians

A. culicifacies

A. d'thali

A. farauti (sp. No. 1)

A. filipinae

Pyrethroid*

Vet. Med.	Agr.	DDT	Cyclod.	OP	Carb.	Fumigant	Other
*	<i>A. flavirostris</i>		*				
*	<i>A. fluviatilis</i>	*	*				
*	<i>A. funestus</i>		*				
	Culicidae (cont.)						
*	<i>A. gambiae</i> (sp. A)	*	*				
*	<i>A. gambiae</i> (sp. B)	*	*				
*	<i>A. hyrcanus</i>	*	*	*			
*	<i>A. labranchiae</i>	*	*				
*	<i>A. maculipennis</i>	*	*				
*	<i>A. messeae</i>	*	*	*			
*	<i>A. minimus</i>		*				
*	<i>A. multicolor</i>	*	*				
*	<i>A. neomaculipalpis</i>		*				
*	<i>A. nili</i>		*				
*	<i>A. nunez-tovari</i>	*					
*	<i>A. pharaoensis</i>	*	*				
*	<i>A. philippinensis</i>	*	*				
*	<i>A. pseudopunctipennis</i>	*	*				
*	<i>A. pulcherrimus</i>	*	*				
*	<i>A. quadrimaculatus</i>	*	*				
*	<i>A. rangeli</i>		*				
*	<i>A. rufipes</i>		*				
*	<i>A. sacharovi</i>	*	*	*	*		
*	<i>A. sergenti</i>		*				
*	<i>A. sinensis</i>	*	*	*			
*	<i>A. splendidus</i>		*				
*	<i>A. stephensi</i>	*	*				
*	<i>A. strodei</i>		*				
*	<i>A. subpictus</i>	*	*				
*	<i>A. sundaicus</i>	*	*				
*	<i>A. triannulatus</i>		*				
*	<i>A. vagus</i>	*	*				
*	<i>Armigeres obturbans</i>	*	*	*			
*	<i>A. subalbatus</i>	*	*	*			
*	<i>Culex annulus</i>	*	*	*			
*	<i>C. coronator</i>	*					

<u>Vet. Med.</u>	<u>Agr.</u>	<u>DDT</u>	<u>Cyclod.</u>	<u>OP</u>	<u>Carb.</u>	<u>Fumigant</u>	<u>Other</u>
		Simuliidae					
	*	<i>Culicoides funus</i>		*			
	*	<i>Simulium aokii</i>	*				
	*	<i>S. damnosum</i>	*				
	*	<i>S. fuscum</i>	*				
	*	<i>S. mixtum</i>	*				
	*	<i>S. pruatum</i>			*		
	*	<i>S. tuberosum</i>	*				
	*	<i>S. venustum</i>	*				
		Syrphidae					
*		<i>Eumerus strigatus</i>		*			
*		<i>Merodon equestris</i>		*			
		Tachinidae					
		<i>Siphona irritans</i>	+	+			
		Tephritidae					
*		<i>Ceratitis capitata</i>	+	+			
*		<i>Rhagoletis completa</i>					Cryolite*
		EPHEMEROPTERA					
		Ephemeridae					
*		<i>Stenonoma fuscum</i>	*				
		Heptageniidae					
*		<i>Heptagenia hebe</i>	*				
		HEMIPTERA/HETEROPTERA					
		Berytidae					
*		<i>Aeneolamia varia</i>		+			
		Cimicidae					
	*	<i>Cimex hemipterus</i>	*	*			
	*	<i>C. lectularius</i>	*	*			*

Vet.
Med.

Agr.	DDT	Cyclod.	OP	Carb.	Fumigant	Other
*		*				
<i>C. fragariae</i>						
<i>Chromaphis juglandica</i>			*			
<i>Eriosoma lanigerum</i>		*				
<i>Hyalopterus pruni</i>			*			
<i>Macrosiphum euphorbiae</i>			+			
<i>Myzus cerasi</i>			*			
<i>M. persicae</i>	*	*	*	+		
<i>Phorodon humuli</i>			*	*		
<i>Rhopalosiphum padi</i>			+			
<i>Sapaphis plantaginis</i>			*			
<i>S. pyri</i>			*			
<i>Schizaphis graminum</i>			+			
<i>Therioaphis maculata</i>			*			
Cercopidae						
<i>Aeneolamia varia</i>		*				
Cicadellidae						
<i>Delphacodes striatella</i>		*				
<i>Erythroneura comes</i>	+					
<i>E. elegantula</i>	*		*			
<i>E. lawsoniana</i>	*					
<i>E. variabilis</i>	*					
<i>Laodelphax striatellus</i>		*	*	*		
<i>Nephotettix bipunctatus</i>	+		*			
<i>N. cincticeps</i>			*	*		
<i>Nilaparvatus lugens</i>	+	*	*			
<i>Typhlocyba pomaria</i>	*					
Coccidae						
<i>Coccus pseudomagnoliarum</i>					HCN*	
<i>Saissetia oleae</i>					HCN*	
Diaspididae						
<i>Aonidiella aurantii</i>			+		HCN*	
<i>Aspidiotus perniciosus</i>						Lime sulfur*
<i>Chrysomphalus ficus</i>			+			

*	Fulgoridae <i>Pyrilla perpusilla</i>	+		
*	Pseudococcidae <i>Planococcus citri</i>		+	
*	Psyllidae <i>Psylla pyricola</i>	*	*	*
HYMENOPTERA				
*	Apidae <i>Apis mellifera</i>	*		
*	Formicidae <i>Atta sexdens</i>	+		
LEPIDOPTERA				
*	Arctiidae <i>Estigmene acraea</i>	*		
*	Crambidae <i>Chilo suppressalis</i>	*	*	
*	<i>Diatraea saccharalis</i>	*		
*	Gelechiidae <i>Anarsia lineatella</i>			Lead arsenate*
*	<i>Pectinophora gossypiella</i>		+	+
*	<i>Phthorimaea operculella</i>	*	+	
*	<i>Sitotroga cerealella</i>	*		
*	<i>Stegasta basquella</i>	+		
*	Hepialidae <i>Oncopera intricata</i>	+		
*	<i>O. rufobrunnea</i>	+		

Vet. Med.	Agr.	DDT	Cyclod.	OP	Carb.	Fumigant	Other
	Lymantriidae						
*	<i>Porthetria dispar</i>	*	*				
	Lyonetiidae						
*	<i>Bucculatrix thurberiella</i>	+	*	+	+		
*	<i>Phyllocnis citrella</i>			+			
	Noctuidae						
*	<i>Agrotis ipsilon</i>		*				
*	<i>Alabama argillacea</i>	+	*				
*	<i>Anomis texana</i>		+				
*	<i>Cosmophila flava</i>	*	*				
*	<i>Earias biplaga</i>	*	*				
*	<i>E. insulana</i>	*	*				
*	<i>Euxoa detersa</i>		*				
*	<i>E. messoria</i>		*				
*	<i>Heliothis armigera</i>	*	*	*	*		
*	<i>H. virescens</i>	*	*	*	*		
*	<i>H. zea</i>	*	*	*	*		
*	<i>Phlogophora meticulosa</i>			+			
*	<i>Plusia brassicae</i>	+			+		
*	<i>P. gamma</i>		+	+			
*	<i>Pseudoplusia includens</i>	+		+			
*	<i>Spodoptera exigua</i>	*	+	*	+		
*	<i>S. frugiperda</i>	+	+				
*	<i>S. littoralis</i>	*	*	*	*		
*	<i>Trichoplusia ni</i>	*	*	*	*		
	Olethreutidae						
*	<i>Carpocapsa pomonella</i>	*		+			Lead arsenate*
*	<i>Grapholitha molesta</i>	*					
*	<i>Paralobesia botrana</i>	*					
	Phycitidae						
*	<i>Ephestia cautella</i>			*			Pyrethrins*
*	<i>Plodia interpunctella</i>			*			Pyrethrins*

Vet. Med.	Agr.		DDT	Cyclod.	OP	Carb.	Fumigant	Other
		ORTHOPTERA						
		Blattidae						
*		<i>Blattella germanica</i>	*	*	*	*		
*		<i>Blatta orientalis</i>	*					
*		<i>Periplaneta brunnea</i>	*					
		SIPHONAPTERA						
		Pulicidae						
*		<i>Ctenocephalides canis</i>	*					
*		<i>C. felis</i>	*					
*		<i>Pulex irritans</i>	*	*				
*		<i>Xenopsylla astia</i>	*	*				
*		<i>X. cheopis</i>	*	*	*			
		THYSANOPTERA						
		Thripidae						
*		<i>Chaetanaphothrips orchidii</i>		+				
*		<i>Diarthrothrips coffeae</i>	*					
*		<i>Scirtothrips citri</i>	*	*				Tartar emetic*
*		<i>Taeniothrips simplex</i>						Tartar emetic*
*		<i>Thrips tabaci</i>	*					

¹ See footnote 1 in Table 3.

Table 5.—Known or suggested factors influencing the selection of resistance to insecticides in field populations.

A. Genetic

1. Frequency of *R* alleles
2. Number of *R* alleles
3. Dominance of *R* alleles
4. Penetrance; expressivity; interactions of *R* alleles
5. Past selection by other chemicals
6. Extent of integration of *R* genome with fitness factors

B. Biological

a. Biotic

1. Generation turn-over
2. Offspring per generation
3. Mongamy/polygamy; parthenogenesis

b. Behavioral

1. Isolation; mobility; migration
2. Monophagy/polyphagy
3. Fortuitous survival; refugia

C. Operational

a. The chemical

1. Chemical nature of pesticide
2. Relationship to earlier used chemicals
3. Persistence of residues; formulation

b. The application

1. Application threshold
2. Selection threshold
3. Life stage(s) selected
4. Mode of application
5. Space-limited selection
6. Alternating selection

For an account and costs of socio-economic disruptions, see Adkisson (1971). Finally, in the human health sector, resistance in *Anopheles* species has required the re-orientation or deferment of malaria eradication campaigns. At a recent meeting of the WHO Expert Committee on Insecticides it was concluded that "resistance is probably the biggest single obstacle in the struggle against vector-borne disease and is mainly responsible for preventing successful malaria eradication in many countries" (WHO 1976).

Frequency of R Genes in Resistant Populations

No information is available on the threshold of *R* gene frequency at which failures to control a pest population occur. Such studies are now feasible in certain anopheline mosquitoes with the development of diagnostic tests which identify the frequency of susceptible genotypes. For instance, by utilizing this approach, Hamon et al. (1968) estimated that 11% of *A. funestus* females in southwestern Upper Volta in December 1967 were dieldrin-resistant. Similar information may be extrapolated from numerous data (Brown and Pal 1971) showing the percentage mortality of *A. gambiae* treated with 0.4% dieldrin in WHO tests.

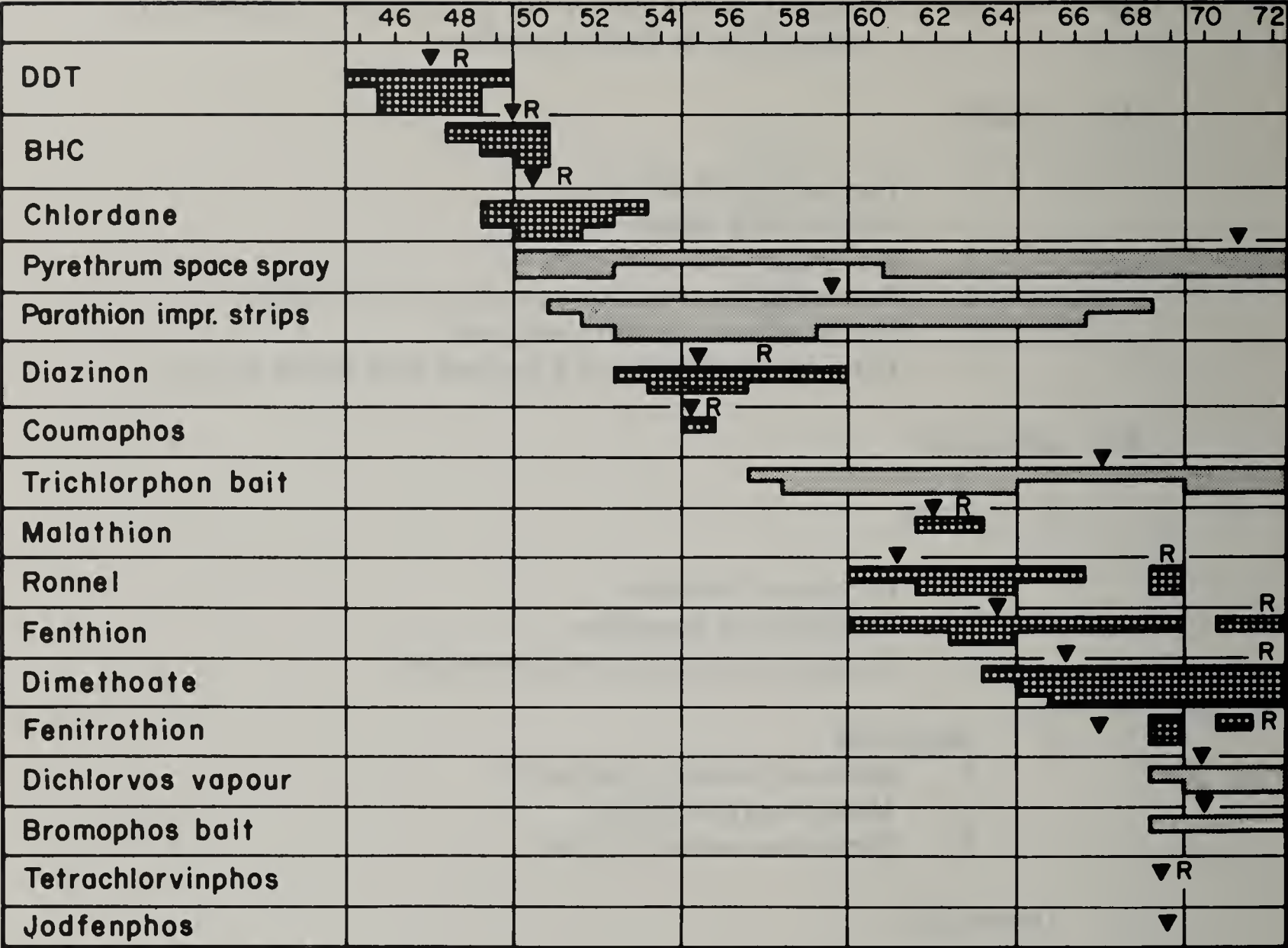


Fig. 2. —Countrywide use of insecticides for housefly control on Danish farms 1945-1972 and development of resistance (adapted from Keiding 1974).

During 1970-71 extensive susceptibility tests were carried out in numerous areas of India to determine DDT resistance in *A. culicifacies*. Of 158 reports of results submitted to WHO (private communication), all but 1 showed that the population was “resistant.”² Calculations from these returns show that of the 8,282 mosquitoes tested the average kill, i.e., the frequency of susceptible phenotypes, was 44%. Without necessarily assuming a steady state of resistance, it may be calculated by the Hardy Weinberg formula that the frequency of *R* genes during the period of tests was .34. Similar tests on *A. albimanus* with DDT or propoxur in 1970-72 indicate that in certain areas of El Salvador the DDT-*R* gene frequency was as high as .80 (e.g., at La Union 1972) and the propoxur-*R* gene .48 (e.g., at La Paz 1971).

The ability to detect resistant phenotypes and to calculate *R* gene frequencies in a given population would constitute an important advance in monitoring the effect of pest control practices on the evolution of resistance.

Evolution of Cross- and Multiple Resistance

Cross-resistance, enabling a resistant population to survive exposure to related chemicals due to the action of a given *R* mechanism, and multiple resistance, which results from the co-existence of several *R* mechanisms protecting against unrelated insecticides, have strongly depleted the available insecticide resources for a number of key pests. Keiding (1974) has illustrated effectively the gradual depletion of insecticides against houseflies in Denmark since 1945 (Fig. 2). More recently he also reported the development of resistance to pyrethroid insecticides under field conditions (Keiding 1974). Extensive multiple resistance has also been reported in field populations of several other species including *Culex tarsalis* (Georghiou et al. 1969), *C. fatigans* (Georghiou et al. 1975), and *Aedes nigromaculis* (Brown et al. 1963) in California, *Anopheles albimanus* in El Salvador (Georghiou

²Survival on test papers treated with 4% DDT was less than 80%.

et al. 1974³, *Nephotettix cincticeps* (Iwata and Hama 1972) in Japan, *Spodoptera littoralis* in the Arab Republic of Egypt, several species of mites and ticks, and others. In most cases such extensive multiresistance is due to the sequential selection of populations with replacement insecticides (Sawicki 1975, Georgiou and Hawley 1971). Each new insecticide selects one or more mechanisms of resistance, and each mechanism usually confers cross-resistance to several other insecticides. In this manner, sequential introduction of alternative compounds can lead to widespread multiple resistance which often includes the supportive retention of resistance to discontinued chemicals (Georgiou and Hawley 1971). For a discussion of the genetics of resistance in sequentially-selected populations of houseflies, see Sawicki (1975).

Emergence of Target Site Insensitivity

Although a discussion of the mechanisms of resistance is beyond the scope of this paper, attention must be drawn to the increasing appearance of strains of arthropods whose resistance to organophosphorus or carbamate insecticides is due to decreased sensitivity of the target site — acetylcholinesterase. This mechanism of resistance was known to exist only in certain tetranychid mites (Smissaert 1964, Ballantyne and Harrison 1967) and the cattle tick, *Boophilus microplus* (Lee and Batham 1966, Roulston et al. 1968). However, in recent years it has been observed also in insects, and it is now found in field populations of the green rice leafhopper, *Nephotettix cincticeps*, in Japan (Hama and Iwata 1971), the housefly in Denmark (Devonshire 1975) and *Anopheles albimanus* in Central America (Ayad and Georgiou 1975). While resistance conferred by this mechanism in houseflies was reported to be of low level (Sawicki 1975), in the leafhopper resistance is higher and involves several organophosphates and carbamates (Iwata and Hama 1972). The highest levels were found in *A. albimanus*, amounting to >1000X toward propoxur and 84X toward parathion (Ayad and Georgiou 1975) and also extending to several other carbamates and organophosphates. This mechanism in *A. albimanus* is due to a single gene allele (Georgiou et al. 1974³), and is suspected to have evolved in response to extremely severe indirect selection pressure from agricultural sprays. By “overpowering” the usual metabolic defense mechanisms, such selection has enabled the far more efficient AChE-R mechanism to predominate. This development may serve as a forewarning of a possible direction in the evolution of organophosphorus and carbamate resistance where selection pressure exceeds the capacity of metabolic defenses in a population.

Factors Influencing Selection of Resistance

The rate of development of resistance in populations has been examined in a large number of cases involving selection under laboratory conditions. The primary conclusion emerging from these studies is that in most cases resistance evolves gradually at first, during a period of integration of various background ancillary factors in the genome of the population, and subsequently at a faster rate to a maximal level which is dependent on the phenotypic expression of the *R* gene(s) in the resistant homozygote. Additional major or minor genes for resistance may be selected subsequently, depending on the extent of pressure or the occurrence of outcrossing with introduced individuals. It must be stressed, however, that while such studies produce essential material for the determination of the mechanisms and spectrum of resistance, they do not provide all the information necessary for the prognosis of the evolution of resistance under field conditions.

The gradual depletion of effective organophosphates and carbamates, the appearance of pyrethroid resistance (Keiding 1974), and the demonstrations that resistance can also involve juvenile hormone mimics (Cerf and Georgiou 1974a, Brown and Brown 1974, review by Vinson and Plapp 1974) and chitin synthesis inhibitors (Cerf and Georgiou 1974b) have focused sharper attention on the need for pest management practices which can extend the useful life of available insecticides. The question thus raised is whether selection for resistance can indeed be slowed or avoided entirely by judicious choice and use of insecticides.

A number of researchers, mostly economists and statisticians, are now attempting to construct computer models which incorporate pesticide resistance as a consideration in pest management

³Georgiou, G.P., V. Ariaratnam, H. Ayad, and B. Betzios. 1974. Present status of research on resistance to carbamate and organophosphorus insecticides in *A. albimanus*. WHO/VBC/74.508, 9 pp.

(Heuth and Regev 1974, Taylor and Headley 1975, Gutierrez et al. 1976). However, whether the management plan is the product of a computer, or is based entirely on the discretionary choice of the individual farmer, the obvious questions which must be considered remain the same, namely, which are the rate-determining factors in the evolution of resistance in a given population?

In Table 5 various factors which are known or presumed to influence the kinetics of resistance are grouped under 3 categories – genetic, biological and operational. Factors in the first two categories are beyond the operator's control; however, knowledge of their contribution serves in assessing the "resistance risk," i.e., the propensity for resistance inherent in a population. Factors in category C are under the direct control of the operator and could be given greater or lesser emphasis depending on the assessment of the resistance risk revealed from categories A and B. The relative influence of changes within each factor have been examined quantitatively by Georgiou and Taylor (1976, unpublished). Some of the more important factors are discussed briefly below.

Genetic Factors

Obviously each factor in this category would have a positive effect on the speed of selection of a resistant population. The frequency of *R* alleles would be expected to be originally low, possibly near 0.01 and 0.0001, if it is assumed that they are selected against in the absence of insecticides, and that their existence is due to recurrent mutation. Dominance of the *R* allele would favor more rapid selection, and the degree of resistance conferred by *R* would determine the gene frequency at which control failures are experienced in the field.

The extent of integration of fitness factors in the *R* genome would be expected to improve with continued selection and outcrossing to peripheral populations. Several studies have shown that with few exceptions (e.g., dieldrin) resistant populations demonstrate lower fitness (Shaw and Lloyd 1969, McEnroe and Naegele 1968) but with continued selection, fitness may improve by coadaptation of the *R* genome, thus resulting in more stable resistance (Abedi and Brown 1960, Keiding 1963, 1967).

Biological Factors

The biological factors in category B (Table 5) are more easily measurable and hence their role in resistance development can be more clearly assessed.

The influence of generation turn-over on the rate of development of resistance is self-evident. In a temporal sense, the larger the number of generations per year the faster the evolution of resistance, assuming that selection is applied in each generation. As an illustration, the fruit tree mite, *Panonychus ulmi*, with as many as 10 generations per year, has developed resistance rapidly to many groups of insecticides (Table 4) whereas *Bryobia rubrioculus*, also on fruit trees, but with usually only 2 generations per year, has yet to be reported as resistant. In a different situation, root maggots, which complete 3-4 generations per year, evolved resistance to cyclodienes within a few years of exposure (e.g., *Hylemya antiqua*, 1957, *H. brassicae*, 1960, *H. platura*, 1964) while the northern corn rootworm, *Diabrotica longicornis*, with only one generation per year, required 8-10 years to develop cyclodiene resistance (Patel and Apple 1966). Similar delays in resistance development have been found in other univoltine species such as the European chafer, *Amphimallon majalis*, and the Japanese beetle, *Popillia japonica*, which manifested chlordane resistance after 9 and 14 years of control, respectively (Tashiro et al. 1971, Tashiro and Neuhauser 1973, Niemczyk and Lawrence 1973, Niemczyk 1975). It would be safe to predict, I believe, that none of us will be present when the 17-year locust, *Magicalcada septendecim*, will have developed resistance.

No information is available on the influence of polygamy on the evolution of resistance. It is suspected, however, that the opportunity for subsequent hybridization with susceptible immigrants, whose frequency in an area would be expected to gradually increase following a pesticide application, should delay the evolution of resistance.

Parthenogenesis might be expected to give rise to clones with uniform resistance, although it would also preclude hybridization and the consequent accumulation of interacting *R* factors.

Behavioral factors could have a decisive role as determinants of resistance. Mobility and migration tend to dilute the frequency of *R* genes among survivors of a treatment so that the evolution of resistance in comparable situations may be expected to be commensurate with the relative isolation of an inbreeding population. For the same reason, polyphagy would tend to delay resistance if a population is only partially selected by also frequenting non-treated hosts. In South

Africa, resistance in ticks of livestock appeared first in one-host species, followed later by two and three-host species (Wharton and Roulston 1970, Whitehead and Baker 1961).

A factor which has been largely overlooked to date is that of fortuitous survival of certain individuals in a treated population. Not all survivors have necessarily been reached by a chemical treatment. Depending on the behavioral characteristics of the species, a proportion of a treated population may be in refugia, thus escaping selection. Refugia could consist of plant tissues, distorted foliage or growth buds, erineum, or may represent a physiological state of lower susceptibility (diapause, pupation in soil, etc.). It can be demonstrated that the larger the ratio of fortuitous survivors to exposed survivors, the slower the evolution of resistance. The citrus bud mite, *Aceria sheldoni* (Eriophyidae) which regularly inhabits citrus bud tissues, has yet to develop resistance, while the surface feeder citrus rust mite, *Phyllocoptruta oleivora*, has been reported to have become resistant to zineb.

Operational Factors

It has become increasingly evident that the greatest opportunities for countering the evolution of resistance depend on our ability to limit the degree of selection pressure according to the resistance propensity characteristics of the target population. Under category C in Table 5 are listed several factors which are under the operator's discretion, and therefore can be modified to the extent necessary to reduce the degree of selection pressure. The importance of many of the factors listed is self-evident and can be thoroughly documented with examples from the published literature. In the most extreme situation, resistance may be expected to evolve most rapidly where the following conditions prevail: (a) a *residual* insecticide is applied which is *closely related* to an earlier-used chemical (b) the compound has *prolonged* environmental persistence (c) or is applied in a slow-release formulation; (d) applications are prescribed at a *low threshold of population* density; (e) the treatment *reaches and selects a high percentage* of the population; (f) selection is directed against *larvae*, or worse still against *both larvae and adults*; (g) a *thorough application* is made; (h) a *geographically large area* is covered, and (i) selection is applied against every generation of the population.

Conclusion

The rapid increase in cases of resistance to pesticides indicates that the continuation of present chemical control practices inevitably leads to exhaustion of available pesticide resources against key pest species. New chemical groups with distinctly novel mode of action are urgently needed. It is clear, however, that a greater understanding of the factors which govern the intensity of selection of field populations for resistance could lead to far more permanently successful use of chemicals within the framework of integrated pest management than heretofore practiced.

To paraphrase a statement made by Dr. A.W.A. Brown (1968) nearly 8 years ago, "By understanding the biochemical, genetical *as well as the ecological parameters* of resistance . . . we should be able to meet the challenge."

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FAO Activities in the Field of Pesticide Resistance

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ABSTRACT

A working party on resistance of agricultural pests to pesticides was established in 1963 to advise and assist FAO on all matters related to pest resistance to pesticides. It, and the Panel that has recently succeeded it, have since met on 11 occasions (i) to consider the nature of resistance, (ii) to carry out world surveys of resistance, (iii) to develop standardised methods for the detection and measurement of resistance, (iv) to arrange for the dissemination of information on resistance and (v) to stimulate the development of countermeasures.

This paper provides an historical review of these activities.

1. *Early History*

At a time when many bodies, including the United Nations Food and Agriculture Organization, are reviewing programmes that have been in progress for some years, it is appropriate to ask what has FAO achieved in the field of pesticide resistance and, indeed, in retrospect, whether it should have become involved in this field.

A Working Party on Resistance of Pests to Pesticides was established on July 25, 1963 by the Director-General of FAO as an outcome of the recommendations of the FAO Conference on Pesticides in Agriculture (FAO 1962). After reviewing the various problems facing the use of pesticides in agriculture, that Conference urged the early establishment of three working parties. One was to deal with pesticide residues, a second with registration, approval and labelling of pesticides, and the third with resistance of pests to pesticides. In the context of this 15th International Congress of Entomology it is appropriate to concentrate heavily upon aspects of resistance concerning arthropods although, particularly in more recent years, significant attention has been paid by the Working Party to resistance in other organisms.

As pointed out by the Resistance Working Party in its first report (FAO 1967a), the most important single property of a pesticide is its effectiveness against the pest. This property is, therefore, quite basic to any further consideration of economics, residues, occupational hazards or legislative control. Thirty years ago it was widely assumed, not unreasonably for those times, that once the pesticidal properties of a new compound had been established, these would provide a good indication of its value for all time. The appearance of the powerful new synthetic insecticides like DDT, gamma-BHC, dieldrin and parathion seemed to promise permanent ability to control the majority of agricultural pests. In quite a dramatic way this assumption has proved not to be valid. An excellent pesticide for a particular job today may be virtually useless within a few years, or sometimes even months, because of the emergence of a resistant strain of the pest. The levels of resistance attained are at times spectacularly high, so that control fails completely in the field and, in the laboratory the insects are found to have become virtually insensitive to the insecticide. Even low levels of resistance may have serious practical implications. An increase by a factor of four or five (or sometimes even less) in the lethal dose for 50% of the population may either render control uneconomic or else result in increasing the residue problem and toxicological hazard, through a predictable tendency of the operator to repeat the treatment, perhaps even with an increased rate of application as well.

The terms of reference of the FAO Working Party of Experts on Resistance of Pests to Pesticides were:

To advise and assist the Director-General on all matters related to pest resistance to pesticides, with particular reference to:

- (a) the development and application of standardized methods for the detection and evaluation of resistance;
- (b) the collection and interpretation of information on the occurrence of resistance; and
- (c) the evaluation and use of alternative existing pesticides with particular reference to resistant strains.

The size of the Working Party has varied from four to seven. In addition, it has been ably supported by experts from the FAO Secretariat and by knowledgeable observers from the World Health Organization (WHO) and GIFAP (Groupement International des Associations Nationales de Fabricants de Pesticides) and from Universities. It has held ten meetings, one each year from 1965 to 1974, and has submitted reports (1967a,b, 1968, 1969a, 1970a, 1971a,b, 1973a,b, 1974a) on each to the Director-General of FAO who, in turn has circulated them to member countries. As a result of the initiative of the seventh meeting (FAO 1971b) where viruses pathogenic to insects were considered to be a possible means of control of some major pests whose resistance had emerged as a problem, the eighth meeting was a joint one with WHO experts to discuss the use of viruses for the control of insect pests and disease vectors (FAO 1973a).

Following a review of FAO expert advisory groups in 1975 the Working Party has now become the FAO Panel of Experts on Pest Resistance to Pesticides and Crop Loss Assessment.

Its terms of reference relating to resistance are:

To advise and assist the Director-General on all aspects related to pest and plant pathogen resistance to pesticides, as well as on resistance to pesticides in non-target organisms and the problem of herbicide-resistant weed flora changes under intensive herbicide use, including:

- (i) laboratory test methods for determining the pesticide susceptibility of pests of agricultural importance;
- (ii) surveys of pesticide-resistant species;
- (iii) development and use of alternative methods of pest control. The first session of this panel has just been held. The major activities of the Working Party and Panel fall under five headings:
 - (i) The nature of resistance.
 - (ii) World surveys of the incidence, importance and spread of resistance in agricultural (including veterinary) pests.
 - (iii) Standardized methods for the detection and measurement of resistance.
 - (iv) The dissemination of information on resistance and stimulation of work in this field.
 - (v) Development of countermeasures.

2. The Nature of Resistance

The pioneering work of WHO over the previous decade provided a valuable basis for the first meeting in 1965 of the FAO Working Party to agree upon the definition of resistance as “a decreased response of a population of an animal or plant species to a pesticide or a control agent as a result of their application” (FAO 1967a). It was possible from the start to accept that populations become resistant because of the selection by pesticides of individuals with a genetic constitution that permitted them to survive and reproduce. Physiological and behaviouristic resistance were distinguished (although the latter is rare, or at least very poorly documented, in agricultural pests). Also noted were cross resistance (whereby a pest strain develops resistance to two or more pesticides as the result of exposure to one pesticide only) and multiple resistance (the simultaneous resistance of the pest to two or more pesticides as a result of successive or simultaneous exposure to these pesticides).

The biochemical basis of at least some types of resistance was already established and the likelihood had been accepted, that some strains were resistant through the presence of structural barriers in the organism that were poorly permeable or impermeable to the pesticide concerned.

3. *World Surveys of Resistance*

In spite of this sound basis of knowledge and the comprehensive body of information already available on resistance in vectors of human disease as a result of the efforts of WHO, relatively limited information had been collated before 1965 on agricultural pests. True, Brown in 1961 included 65 such pests in his statement "the total number of species with resistant strains had risen since 1945 to the appalling figure of 137." Resistance was "about equally divided between plant-feeding insects and mites, and insects or ticks of public health or veterinary importance." The first of the FAO general world surveys of resistance in agricultural pests was carried out in 1965, with information being sought on species reported, or suspected to be developing, resistance, on pesticides to which resistance had developed, on locality, control history and alternative methods of control used or under trial. A second general world survey was carried out in 1968 and a third is currently in progress and will be summarised in a forthcoming book by H.T. Reynolds and G.P. Georgiou of the Riverside campus of the University of California.

In 1965, 182 pests were included in the lists of the first survey (FAO 1967a) as being resistant or suspected of being resistant and, by 1968, the total had risen to 228 (FAO 1969a). The third incomplete survey has considerably increased that number.

A survey far more ambitious and detailed than any of the preceding was initiated at the seventh meeting of the Working Party (FAO 1971b) which viewed with grave concern the steadily progressing development of resistance in stored grain pests. Over the previous decade or so many countries had come to rely on lindane or malathion as protectants and methyl bromide or phosphine as fumigants to prevent serious loss in storage and to provide clean grain to meet the stringent requirements of international trade. Although there were mounting reports of resistance to lindane and malathion in particular, there was no knowledge of their relevance to control failures nor of the possibility of switching to alternative effective materials. The need for effective protection of stored grain against insect attack is self evident, when it is recognised that this is the basic foodstuff for the world's rapidly growing population and that losses of 10 percent and more still occur far too frequently in developing countries. FAO undertook a global survey of stored grain pests in 1972 and 1973, in which B.R. Champ visited 61 countries to collect strains of major pests for pesticide resistance monitoring. Some 1600 strains were collected and these, together with strains from 25 other countries, were cultured and tested by C.E. Dyte for resistance to the four toxicants listed above. The results of this survey are in press (Champ and Dyte 1976) and relevant sections of the chemical industry were alerted to the potentially very serious situation at a session specially convened during one of the meetings of the Working Party (FAO 1973b).

It would not be appropriate to cover even the main findings of the survey here, except to say that it has detected in all countries resistance, ranging from a very low to a high level for one or more of the chemicals currently available for grain pest control. In a number of areas the level is already high enough to result in control failure.

Since specific instances of resistance will be dealt with in some detail by other speakers I shall confine myself to listing eight general points that have emerged from the FAO surveys. They refer principally to experience with the numerous arthropod pests involved, although, in the last few years in particular, there has been a steadily growing incidence of resistance in plant pathogenic fungi to systemic fungicides.

(i) Resistance problems of great and sometimes critical importance have arisen in each region where pests have been exposed to heavy selection pressure from pesticides.

(ii) There appears to be a correlation between the general level of pesticide usage in a region and the number of resistance problems that have arisen.

(iii) In many countries with an agricultural economy the key pests of major crops are among those that have developed important resistances.

(iv) Some pest species have developed resistance quite independently in many different parts of the world. This is explained by the fact that genetic factors for resistance are already widespread in the population, even if they only occur initially at very low frequencies.

(v) Some pest species evidently have a genetic diversity that enables them to develop resistance to each of a succession of pesticides that are used against them. Examples include ticks, spider mites and the housefly.

(vi) No instances have been reported where field resistance has declined sufficiently to enable the re-introduction of a formerly effective pesticide to which resistance had developed.

(vii) Although new pests are progressively developing resistance to pesticides the more striking current problem arises from the fact that well known resistance is extending both geographically and in terms of the number of chemicals that can no longer be safely or effectively used for pest control.

(viii) Resistance does not usually involve any visible change in the behaviour or morphology of the pest: it is generally caused by subtle changes in the biochemistry or physiology of the pest or by an alteration in the permeability of its membranes.

4. *Standardized Methods for the Detection and Measurement of Resistance*

The monitoring of susceptibility and the early detection of resistance provide a basis for deciding whether alternative means of control should be sought and also for evaluating alternative pesticides. Monitoring may, indeed, serve to eliminate resistance as the cause of a control failure and thus indicate the need to take action other than to change to another pesticide.

Although encouragement was given at the first meeting in 1965 for the FAO Working Party to follow the WHO pattern of developing standardized test methods for detection and measurement of resistance, it was 1967 before the Working Party was able to embark upon a programme of its own for arthropod pests of food and agriculture. About the same time the Entomological Society of America began to investigate standard tests for pests of special importance in North America, beginning with the boll weevil and spider mites: since then the activities of the two bodies have been closely integrated.

The Working Party first prepared a list of pest species for priority attention, based on the economic importance of chemical control for each pest and the degree of impairment of this control that was believed to be due to the development of resistance. For each pest an experienced scientist who was known to have conducted tests with the species in question, was invited to draw up a suitable test procedure. This was then submitted to one or more referees in other institutions who had relevant experience for evaluating the test. Eventually a tentative method was approved by the Working Party and published in the FAO Plant Protection Bulletin, so that experience of its appropriateness and value to workers generally could be assessed (1969b). So far 16 accounts have been published relating to 14 pests or groups of pests (Table 1). Further arthropod pests are currently under consideration.

The primary requirement of a resistance test is that it can be exactly duplicated wherever and whenever required, so that results obtained by different workers are comparable. This means that naturally occurring substrates, such as leaves or grain, are unsatisfactory. Instead, readily obtainable standard materials, such as filter paper, and solvents such as acetone or alcohol must be employed. Although experience is required in the extrapolation of the results of such tests to field situations, it

Table 1.—FAO Tentative Standardised Tests for Resistance.

Method	Test No.	Pest	Published
Impregnated filter paper	6,15	Stored food beetles	1970, 1974
	9	Cocoa mirids	1971
	7	Cattle tick larvae	1971
	14	Sheep blowfly larvae	1974
Topical application	2	Root maggot flies, carrot rust fly	1969
	3	Rice stem borer	1969
	4	Peach-potato aphid	1970
	5	Green rice leafhopper	1970
	8	Egyptian cotton leafworm	1971
	12	Colorado potato beetles	1974
	11	Codling moth	1974
	13	Locust adults	1974
	14	Sheep blowfly adults	1974
Aqueous Suspension (dip)	10	Spider mites	1974
Fumigant	16	Stored food beetles	1975

does become possible to predict that laboratory-determined resistance exceeding a certain level and frequency for a particular pest and chemical will lead to control failure in the field.

Whereas it was recognized that the great variety of the pest species involved would not permit a single test method to be adopted for all, it was also noted that much of the diversity of techniques already reported was unnecessary. The early WHO tests nearly all depend on the self-dosing of insects exposed to a toxic deposit and, in spite of some imprecision in dosage that this involved, this method was adopted in 4 of the FAO tests. However, there are advantages in employing a topical application technique, in which the actual dose applied to each insect is known. This may be achieved by applying it either with a micro-syringe or a self-filling micro-capillary and such methods are involved in 9 FAO tests. One of the tests is for the evaluation of resistance of grain beetles to fumigants and another is a dip method for aphids, using an aqueous suspension.

In general, the stage of the pest most convenient for handling has been selected for the test. However, it is preferable that this should be the life history stage on which the pesticide exerts its main selective action, because the levels of resistance development by different stages of the same pest may differ widely (Arnold and Whitten 1975).

Wherever possible, in measuring resistance a quantal response method based on a geometric series of dosages has been recommended, with resulting percentage mortality values, corrected for control mortality, being plotted on a probit scale against dosage on a logarithmic scale. This provides comprehensive information on the distribution in the population of susceptibility to the toxicant. However, for greater speed and convenience when regular monitoring is being used to detect the first appearance of resistance, batches of insects may be exposed to a single “discriminating” dose. This approach is applicable to populations where the probit regression line does not deviate too far from vertical. As a working guide, a discriminating dose may be chosen which is double that which has consistently given complete kills of all batches of susceptible insects. Alternatively, as in the test for rust red flour beetles (FAO 1970d), the dose required for 99.9% mortality can be chosen. When survivors begin to appear regularly it is necessary to revert to more comprehensive testing in order to explore the changed resistance status of the population.

In relation to standardized tests for resistance in agricultural pests other than arthropods, a WHO feeding test for resistance to anticoagulants in rats and mice is available (WHO 1970) and has permitted the unequivocal demonstration of resistance in seven rodent species. The other important group of pest organisms where resistance has reached serious proportions is the fungi. Although there were a few early records, the number of reports of resistance (163) has grown apace along with the rapidly increasing use of systemic organic fungicides (especially the benzimidazoles) over the last decade. Standardized methods will be a valuable aid in the future to workers in this field. Surprisingly few instances (only 17) of resistance of weeds to herbicides have been reported, considering their widespread usage and so far there appears to be little need for standard tests. There appear to be no records of resistance among nematodes attacking plants, although there is some resistance among helminths resident in the digestive tract of mammals. However, no standard test methods have yet been adopted.

5. The Dissemination of Information on Resistance and Stimulation of Work in this Field

The Working Party considered from time to time the many problems relating to the effective dissemination of information relating to pesticide resistance, and particularly to explaining its nature and the vital importance of its early detection. Whereas the scientist was tolerably well catered for in specific fields, there was little appropriate material available to administrators and technical and advisory specialists in crop protection. There was, for example, no general account of the nature, occurrence and significance of pesticide resistance in pests of agricultural importance nor about countermeasures that could be taken.

Two publications of the FAO Working Party were directed towards filling the first gap. The first was a general account of the nature and importance of resistance phenomena for biologists, chemists and agricultural extension workers concerned with crop protection. It was designed “to facilitate the early recognition of resistance in field populations, to facilitate the application of suitable countermeasures, and to minimise factors which favour the development of resistance of pests in agriculture” (FAO 1970f). The second is a small, simply-written, model extension leaflet designed for intelligent farmers and extension personnel, explaining resistance, its detection, and the

action needed (Deal 1971). It was designed to serve as a basic text for developing countries to adapt as they thought fit.

An even more ambitious FAO-sponsored publication is in press and another in an advanced state of preparation. The former by B.R. Champ and C.E. Dyte (1976) is an account of the FAO global survey of pesticide susceptibility of stored grain pests and is a major contribution in this field. The latter is a comprehensive monograph on pesticide resistance in agricultural pests by H.T. Reynolds and G.P. Georgiou and will serve for many years as the standard work of reference in this field.

The Working Party and its members have also assisted greatly in disseminating information by organizing or participating in sessions on resistance at international meetings. In the FAO context, the FAO symposium on Resistance of Agricultural Pests to Pesticides (FAO 1970e) and the FAO conference on Ecology in Relation to Plant Pest Control (FAO 1973c) were both attended by participants from many countries and each had significant effects.

A further major impact of the Working Party has been the stimulation of workers in many parts of the world to publish information that would otherwise have been unavailable. Furthermore it has encouraged them to carry out the additional testing needed to authenticate the evidence for what had previously only been locally-recognised control failures in the field.

6. Development of Countermeasures

Two principles are basic to the sensible use of chemicals for pest control, namely (i) to avoid, where practicable, unnecessary selection pressure for resistance and (ii) to anticipate the resistance problem.

With regard to the first principle, the probability of the emergence of a resistant pest population is a function of the frequency, intensity, persistence and extent of pesticide application. These are factors involved in determining whether survivors are resistant rather than just lucky. Pesticide application should be, as far as possible, only on the target area, timed for only the optimal period for the pest(s) involved, and based on an economically significant infestation or threat of infestation rather than applied as a fixed routine. Unnecessarily persistent chemicals should be avoided, so that selection will not continue after the pest has ceased to be important to the plants or animals being protected.

In relation to the second principle, the evaluation of alternative pesticides and, more importantly, of control methods that do not rely upon the use of chemicals, should be undertaken as early as possible. Then if control difficulties arise and resistance is confirmed, sensible countermeasures are available. At present, the simplest, and generally the only immediately available, option (when control fails due to the occurrence of resistance) is to switch to an alternative pesticide to which the pest is susceptible. However, experience gives very good reasons for believing that, sooner or later, resistance to the new pesticide will develop and the sequence will have to be repeated, generally resulting in the introduction of progressively more and more expensive pesticides.

The concept of integrated control (or pest management as I prefer to call it) is now so well known and so widely accepted that it is unnecessary for me to dwell upon its virtues here. However, it is worth recording that this concept was very strongly supported by the Working Party from the outset. Indeed recommendations of its first meeting (FAO 1967a) helped to launch the FAO Symposium on Integrated Pest Control which followed hard on its heels (FAO 1966). From then on the FAO Working Party on Pest Resistance to Pesticides and the more recently formed FAO Panel on Integrated Pest Control have worked closely together, having some members in common and at times holding overlapping meetings.

7. Conclusion

Reviewing the outline, I have presented of Working Party activities based on meetings occupying barely 3 months over the past 11 years I conclude that not only has very considerable progress been achieved during that time in the field of pest resistance to pesticides, but also that the Working Party approach to a problem basic to food and fibre production in most countries of the world, can indeed be a highly effective way of using FAO's resources. Furthermore, without FAO involvement, it is likely that certain important actions would have been quite impossible, for example the development of standard international test methods and the global survey for resistance in grain pests.

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Problems of Resistance in Pests of Field Crops

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The problem of insecticide resistance exists worldwide among insects and mites affecting field crops, ranging from minimal or absent in some developing countries, where use of insecticides has been low, to extremely severe in many developed countries. Cotton is without question the field crop most severely affected by resistance development, but all the field crops are affected to varying degrees. Rice pests, for example, have developed worrisome levels of resistance in several areas of the world, particularly in Japan. Although fewer pests have developed resistance on important field crops like alfalfa, maize and sorghum, often these resistant species represent the perennially serious "key" pests which often require multiple chemical applications each season.

Cotton probably exemplifies the problems accruing from resistance development better than any other single crop, and it seems, therefore, worthwhile to examine the resistance situation on this crop in some detail. It was estimated recently that more total insecticide is applied worldwide to cotton than all other agricultural crops combined. This estimate seems rather high, considering the intensive insecticide use on the vast acreages of rice, vegetables, etc., but it is known that about 47% of the insecticides applied to agricultural crops in the United States is used on cotton (Eichers et al. 1970, Pimentel 1973). We can safely assume, consequently, that selection pressures for resistance development have been exceedingly harsh in many cotton producing areas of the world.

A recent world survey (to be published) conducted by the United Nation Food and Agriculture Organization Panel of Experts on Resistance of Pests to Pesticides found that 33 species of cotton pests have developed resistance. Quite likely there are others, but the results provide a good indication of the prevailing situation nevertheless. The 33 species reported to be resistant at this time compare with 20 species in the survey made by U.N. Food and Agriculture Organization in 1965 (FAO 1967). However, equally and perhaps more serious is the obvious increase in intensity and spread in area of some of the cases in the ten-year interval between the two surveys.

The results of this survey are shown in Table 1.

Resistance of most species is still restricted to relatively small areas, and none is known to be resistant throughout its entire range of distribution. However, a few are resistant throughout most of their range. The boll weevil, for example, is resistant in 10 of the 11 states in which it is known to occur in the United States and is also widely resistant in Mexico and into Central America. Likewise, the cotton leafperforator, *Bucculatrix thurberiella*, has developed resistance in most hot, arid areas of North and South America, conditions which are favorable to maximum population development and to crop damaging levels.

Undoubtedly, other species could be added to this list. Currently there is reason to suspect the early stages of resistance in the pink bollworm, *Pectinophora gossypiella*, to certain organophosphorus insecticides for the first time in cotton producing areas of southern California. Recent evidence indicates, however, that this has already happened in Egypt. Furthermore, surveys of this nature are never complete and can be considered only as indicators of the prevailing situation in the field.

Sometimes subtle effects are noted which involve considerable research time to clarify. An interesting example of this situation is occurring in the Imperial Valley of California at this time. Agromyzid leafminers have never been reported to be pests of cotton insofar as I am aware. Normally, under reasonably effective population regulation by parasites, about 10 years of intensive,

Table 1.—Results of a U.N. Food and Agriculture Organization survey of pesticide resistance development in pests of cotton.

Species	Type of Pesticide	General Locale
<i>Tetranychus arabis</i>	OP	Egypt
<i>T. bimaculatus</i>	OP	Colombia
<i>T. cinnabarinus</i>	OP, Ocl.	U.S.A.
<i>T. (complex of species)</i>	OP, Ocl.	Greece
<i>T. cucurbitacearum</i>	OP	Egypt
<i>T. desertorum</i>	OP	Mexico
<i>T. hydrangea</i>	OP	Mexico
<i>T. pacificus</i>	OP	USA
<i>T. telarius</i>	OP, carbamates, Ocl.	U.S.S.R., USA, Egypt S. America, Africa
<i>T. tumidus</i>	Ocl.	Barbados
<i>T. urticae</i>	OP, Ocl., carbamates	USSR, Greece, Turkey, USA
<i>Anthonomus grandis</i>	Ocl.	Mexico, USA, Venezuela
<i>Eutinobothris brasiliensis</i>	Ocl.	Brazil
<i>Lygus hesperus</i>	Ocl., OP	USA
<i>Pseudatamoscelis seriatis</i>	Ocl.	USA
<i>Dysdercus peruvianus</i>	Ocl.	Peru
<i>Trialeurodes abutilonea</i>	OP	USA
<i>Empoasca bigittula</i>	Ocl., carbamates	Taiwan
<i>Aphis gossypii</i>	OP	USSR, USA, Peru, Zambia
<i>Estigmene acraea</i>	Ocl.	USA
<i>Pectinophora gossypiella</i>	Ocl.	Mexico, USA
<i>Bucculatrix thurberiella</i>	Ocl., OP	Mexico, USA, Peru
<i>Alabama argillacea</i>	Ocl.	USA, Colombia, Venezuela
<i>Anomis texana</i>	Ocl.	Peru
<i>Cosmophila flava</i>	Ocl.	Ivory Coast, Mali
<i>Earias biplaga</i>	Ocl.	Mali
<i>Earias insulana</i>	Ocl.	Mali, Israel, Spain
<i>Heliothis armigera</i>	Ocl., carbamates	USSR, Thailand, Australia
<i>H. virescens</i>	Ocl., OP, carbamates	USA, Peru, Mexico, Colombia
<i>H. zea</i>	Ocl., OP, carbamates	North, Central, South America
<i>Plusia brassicae</i>	Ocl., carbamates	Barbados
<i>Spodoptera exigua</i>	Ocl., OP	USA
<i>Spodoptera littoralis</i>	OP, Ocl., carbamates	Egypt, Turkey, Israel, India
<i>Trichoplusia ni</i>	Ocl., OP	USA

repeated applications of broad-spectrum organophosphorus insecticides for pink bollworm control have almost eliminated parasites of this as yet unidentified agromyzid leaf miner. For the first time in the history of cotton production in this area, an outbreak of this leafmining species is occurring. Although crop damage has not been assessed and may not be serious, it seems highly likely that this agromyzid species has become resistant to the broad-spectrum OP. insecticides currently in use. This is apparently a secondary problem induced by beneficial insect depletion by insecticides which became evident only after the species developed resistance.

In considering the United States specifically, Adkisson (1973) listed three major cotton producing regions and the key pests in each. Each of the three has a different climate and diversity in the cotton ecosystem. These are:

1. The irrigated deserts of the far west where the key pests are the pink bollworm, lygus bugs, and the bollworm.
2. The semiarid regions of the southwestern United States where the bollweevil, fleahopper, bollworm (*Heliothis zea*) and tobacco budworm (*H. virescens*) are the key pests.

3. The humid areas of the midsouthern and southeastern United States where the boll weevil, plant bug, bollworm and tobacco budworm are the key pests.

Recalling the list of resistant species in Table 1, it is noted that each of these key pests in the three cotton production areas have developed resistance to one or more types of pesticides. In each case, the resistance levels are sufficiently high to complicate insecticidal control measures. The situation in neighboring areas of Mexico is quite similar.

The history of insecticide use on cotton in the United States and the development and impact of resistance development was described by Reynolds et al. (1975), National Academy of Sciences (1975). Adkisson (1969, 1972) and Bottrell and Adkisson (in press) described in detail the impact of resistance in southern Texas and northeastern Mexico. This situation is repeated here briefly as it illustrates the extreme effect of resistance upon the cotton producer and supporting industries. The problem began in the mid-1950's when the boll weevil first developed resistance to the organochlorine insecticides and was soon followed by Ocl. resistance in the tobacco budworm and bollworm. Low dosage rates or organophosphorus insecticides, principally methyl parathion but also azinphosmethyl, EPN, malathion and others, were very effective on the boll weevil. The beneficial insects were extremely susceptible to the OP-compounds and applications were more frequent because of the short residual activity of this group of chemicals. Tremendous outbreaks of the *Heliothis* complex followed in the absence of natural enemies. Also, the low OP dosage rates used did not reduce the *Heliothis* populations. It was necessary to use high dosages and to make applications more frequently to maintain maximum yields. Production costs increased, placing the grower in a tighter cost/price squeeze.

It is interesting to note the gradual increase of resistance to methyl parathion by the tobacco budworm in Table 2.

Table 2.—Comparative resistance of the tobacco budworm to methyl parathion.^a

Location	Year	Increase in Resistance
College Station, Texas ^b	1964	Susceptible
College Station, Texas ^b	1968	4X
College Station, Texas ^b	1969	6X
College Station, Texas ^b	1970	14X
College Station, Texas ^b	1971	11X
College Station, Texas ^b	1972	51X
Weslaco, Texas ^b	1968	5X
Weslaco, Texas ^b	1969	11X
Weslaco, Texas ^b	1972	25X
Tampico, Mexico ^c	1969	46X
Tampico, Mexico ^c	1970	61X
Monte, Mexico ^c	1970	201X

^aAdkisson 1974

^bData from Nemec and Adkisson 1973

^cData from Wolfenbarger et al. 1973

The situation at that time was simply that without boll weevil control, farmers could not produce good cotton yields, but with weevil control, tobacco budworm populations increased to the point where successful production was jeopardized. As described by Bottrell and Adkisson (in press), many cotton farmers in this region treated their fields 15, 20 or more times with high dosages of very toxic insecticides, but still suffered grave losses in yield and in some cases fields were never harvested. Others, who obtained good yields, had small profit margins because of high costs of cotton protection. The situation in neighboring areas of Mexico was even worse. Several hundred thousand acres of cotton went out of production for some time. Cotton farms were abandoned, gins, compresses and oil mills ceased operating, farm workers were forced to move elsewhere, and the whole socio/economic structure of communities was affected. Furthermore, the high dosages of toxic

OP-insecticides repeatedly applied resulted in frequent illness of spray applicators and farm workers (Wiseman and Smith 1971).

This extreme situation described above illustrates forcefully the serious implications of pesticide resistance. The boll weevil population is now reduced in late fall by chemical and cultural means, just prior to the weevil entering diapause, to the point where chemicals are only needed late in the following production season. This practice permits beneficial insects to exert population regulation of *Heliothis*. But resistance has created serious problems in other areas of world-cotton production. The very serious problem on cotton in Nicaragua is described in a later paper, which emphasizes the importance of insect pest management in coping with the situation. The development of resistance in *Heliothis armigera* to formerly effective insecticides in the Ord River Valley of northwestern Australia has forced abandonment of cotton production. The Ord River area is far from markets and the resistance problem was, in effect, the "last straw" in reducing production to an unattractive economic status. Insecticidal control in many areas of the world has been greatly complicated by the development of resistance. The notorious cotton leafworm, *Spodoptera littoralis*, is a key pest in several countries of the Middle East. The Arab Republic of Egypt has recurring problems, for example, as this pest inexorably develops resistance to insecticides found to be effective and imported for its control. As insecticides are normally imported and stockpiled prior to the cotton season, when resistance occurs during the season, yield losses often follow before another effective insecticide can be imported. Very commendably, a resistance monitoring system has been initiated which may be able to anticipate resistance sufficiently in advance to be prepared before insecticide failures occur.

Some of the problems accruing from the development of resistance have already been briefly discussed. A few of these are increased costs of protecting cotton with a reduced margin of profit to the farmer, the socio-economic impact of being forced to abandon or drastically reduce cotton production in an area, and health and environmental hazards of more frequent applications and increased dosage rates frequently following resistance development. Many examples of resistance development in non-target pests in the cotton ecosystem could be listed. It is now widely recognized that following resistance development plus the loss of beneficial insects and their regulatory activities, the nontarget, often secondary, pests can assume major pest status, seriously complicating pest control practices. The result is often the need for additional applications of a different insecticide or frequently the use of insecticide combinations, all of which places more selection pressure upon the arthropod population for resistance development.

Clearly, the commercial development and merchandizing of insecticides are affected by resistance. The chemical industry, already troubled by the huge costs and complicated requirements of development to registration and sales, also faces the nagging concern about the potentially short sales life of a newly developed product because of resistance development — this is particularly the case in important pests of major crops such as cotton before investment is regained. The question is no longer "if" resistance develops, but "how soon." A factor facing research entomologists and industry personnel alike is the question of whether to use a new pesticide aggressively and extensively for a shortened lifetime or conservatively for a longer period (Glass and Committee 1976). Competitive products and the need to regain investment and show a profit as quickly as possible normally dictate the former. Some entomologists were optimistic for many years that the insecticide industry would continue to produce new insecticides that would counteract problems created by resistance. The response by industry has indeed been favorable, but the discovery of new compounds that are effective on resistant pests has become much more complex and costly. As a result, the chemical industry has become more cautious in the very difficult decision as to whether or not to develop a new chemical to the point of sales. Certainly the trend in number of new agricultural chemicals appearing in the market place is sharply downward as the cost of developing pesticides is sharply upward (Dow Chemical Company 1976).

Perhaps other concerns which illustrate the problems of resistance development on cotton and other crops should be listed, but the above brief discussion demonstrates the serious implications of the steadily advancing problem.

Although cotton has been used as the primary example of problems created by pesticide resistance, its inexorable development in pests affecting other field crops, although generally less serious than on cotton, is troublesome now and all indications point toward increasing problems in the future. Resistance has not yet developed to a large number of insects affecting production of crops like alfalfa, maize, and sorghum, but, as one might suspect, most species that have developed

resistance are of major importance. However, resistance development in insects affecting rice is more widespread and serious.

Excluding pests of stored rice, the first FAO world-survey in 1965 reported that eight species of insects affecting rice production had become resistant to one or more insecticides; ten years later there are fourteen. The percentage increase in numbers of species is quite similar to the increase in cotton. In the United States only the rice water weevil, *Lissorhoptrus oryzophilus*, has developed resistance (cyclodiene compounds), and *Spodoptera frugiperda* is resistant to this group of compounds in portions of South America. *Tryporyza incertula*, a paddy stem borer, is reported to be resistant to organophosphorus compounds in Peru. The other species reported to have developed resistance are all found in the Asiatic countries and neighboring Pacific islands. Japan reports the most severe cases of resistance, being particularly serious in several virus vectoring species of leafhoppers. Insecticides reported to be no longer effective include Carbaryl, some Ocl.'s, and a large number of OP compounds. Also, the very damaging Asiatic rice borer, *Chilo suppressalis*, is now reported to have developed resistance to a large number of organophosphorus insecticides and to BHC and lindane. The development of resistance in rice pests must be viewed with concern. The continued reports of difficulties with additional pest species, the intensification of the problem as effectiveness of more groups of insecticides are lost, and the increasing size of affected production areas all point toward increasingly serious problems which eventually may affect production.

In field crops such as alfalfa, maize and sorghum, insecticide resistance is not reported to exist in a large number of species. Nevertheless, in some areas, crop protection has been complicated by the development of resistance in one or more major pests. Resistance to the organochlorine and cyclodiene insecticides has developed in populations of the alfalfa weevil, *Hypera postica*, in the United States and in U.S.S.R. In the U.S., these compounds can no longer be applied to this crop (except for methoxychlor) in any case. Organophosphorus resistance is reported in the spotted alfalfa aphid, *Therioaphis maculata*, and in the cowpea aphid, *Aphis craccivora*, in the U.S.A. and U.S.S.R., respectively. *Spodoptera littoralis* resistance in Middle Eastern countries has created problems. Although other cases of resistance have been reported on alfalfa, one of the most troublesome is the problem of lygus bugs, particularly *Lygus hesperus*, in alfalfa seed production. Resistance in this species is reported to organochlorine and several organophosphorus insecticides.

Production of both sorghum and maize is affected to some extent by resistance in the *Heliothis* complex. Several types of rootworms of maize have become resistant to the very effective cyclodiene compounds, particularly in the *Diabrotica* complex in North America. However, use of these compounds has been virtually phased out by regulatory restrictions, but available substitute insecticides do not provide the same degree of effectiveness. Other species that have developed resistance in various areas of the world all provide evidence of crop protection problems. All complicate plant protection on these crops to various degrees.

It is difficult to find any rewarding aspects in the perplexing, often aggravating problems accruing from insecticide resistance, and no easy solution appears to be on the horizon. Entomologists must spend far too much research time in the search for substitute chemicals to counter the steadily worsening problem of resistance — time which could be better spent on the more basic aspects of pest problems affecting these crops. Quite clearly, however, the advancing resistance problem has provided major impetus to the development of insect pest management tactics and programs. Progress in the development of new methods to manage pest populations is encouraging as is the improvement in many of the techniques relied upon in past years. In my view, the application of all our techniques, both old and new, into integrated programs must be our route to cope with resistance. In many respects, we can judge this to be a plus for insecticide resistance.

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Problems of Insecticide Resistance in Insect Vectors of Human Disease

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The control or eradication of many widespread vector-borne diseases of man is to a large extent dependent on the use of pesticides since these were introduced nearly 30 years ago. Their use enabled programmes to be undertaken to control the vectors of malaria, filariasis, dengue fever and leishmaniasis among others. It is increasingly being recognized that resistance of vectors to pesticides is the biggest single obstacle in the struggle against vector-borne disease and is mainly responsible for preventing the successful completion of some of the programmes such as malaria in many countries. The extension and increase in level of resistance to DDT (first detected 28 years ago in the housefly and the common house mosquito) and other organochlorine insecticides together with some concern about environmental contamination had led to the abandonment of these cheap and efficient insecticides in many cases. The change-over to insecticides of other chemical groupings such as organophosphorus and carbamates has involved substantial increases in the cost that entails severe hardship in developing countries unable to defer funds from other urgent needs. Furthermore, in countries that have been able to use newer insecticides, cases of resistance towards them have already appeared, especially where these chemicals were also being used in agriculture. The outlook, with regard to further alternative pesticides, is uncertain because of cross-resistance. Moreover, resistance has also been reported to new generations of insecticides such as insect development inhibitors, chemosterilants and even biological control agents. It is clear from the investigations carried out during the past many years on the problem of insecticide resistance that there is no single or simple solution available to meet the problem and therefore a constant vigilance will have to be maintained. As long as insecticides remain the principal tool for the control of disease it seems inevitable that resistance will be a serious threat to the future progress. The implications are quite clear that no major breakthrough is expected in the future, although we have much more understanding of the problem in the light of which it may be possible to develop realistic policies for future vector control to meet the problem as effectively as possible.

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Monitoring of Resistance

Since about 1960 WHO has been able to follow the global situation of the incidence of insecticide resistance by means of reports received from the users of widely distributed standard susceptibility test kits sponsored by WHO. These tests are available for practically all major vectors of disease. To process the massive amount of data available a computer programme has been developed by which information can now be retrieved by countries, species and insecticides in current use. The interpretation of data is based on the LC_{50} and LC_{95} determination as well as LT_{50} and LT_{95} determination especially for organophosphorus and carbamate insecticides. With additional experience it has now been possible to introduce the diagnostic dosages of various insecticides where field populations can be monitored. These data though providing definite proof of resistance (especially valuable as an early warning) cannot, however, convey the impact of individual cases on actual vector control. Therefore, WHO made periodic surveys of the impact of insecticide resistance on control of vectors and vector-borne disease. In 1968 (1) and 1975 (2) an attempt was made to obtain this information by means of a questionnaire which sought information on (a) control schemes in various countries (insecticides used and scale of operations), (b) resistance developed (insecticide group and whether suspected or confirmed), (c) effects on control (moderate or severe, which insecticide(s) had been abandoned, the possible increase of disease as a result of resistance). For the most serious problems in vector control further details were obtained by subsequent correspondence with the informants. In addition the particularly important sphere of resistance in malaria vectors was investigated by a further questionnaire which was dispatched to 14 countries in January 1975 inviting officers in charge of anti-malaria programmes to prepare position papers on proper surveys of the dimensions of the vector resistance problem and its implications throughout the programme history up to the present. The information gathered from all these sources as well as from other available information (3), was recently analyzed by the WHO Expert Committee on Resistance of Vectors and Reservoirs to Pesticides (4) and a brief summary is presented in the following sections.

Part I: The Anopheline Vectors of Malaria

In 14 countries where information is available indicating that insecticide resistance has created an operation problem, the total population of areas affected by insecticide resistance is estimated to be 256,111,000, which represents about one-third of the total population of the malarious areas (870,671,000) (see Table 1).

The Present Status

The African Region. — *A. gambiae* s.l. is the main malaria vector in the African Region, and, together with *A. funestus* is responsible for the great bulk of malaria transmission there. Dieldrin resistance in *A. gambiae* s.l. has been reported from West Africa for the last 20 years and more recently from certain parts of East Africa, namely Kenya and Madagascar. It appeared that *A. gambiae* has remained susceptible to DDT until a very high level of resistance to this insecticide was reported from Bobo Dioulasso, Upper Volta in 1968 (5) in species A of this complex. This species was completely susceptible in this area to DDT during 1953-1960. Later, DDT resistance was reported in species A from Togo where DDT has been applied in limited field trials for the control of malaria (Bakri, unpublished report to WHO). Further reports indicated the presence of DDT resistance in species B in Senegal as was detected at Thiès in 1968 where DDT spraying was applied and the density of the species remained quite high (Morcos, unpublished report to WHO). Further records of DDT resistance have been received from Lagos State in Nigeria (Bakri and Ototoju, unpublished report to WHO), Cameroon, Guinea and Benin. DDT resistance has been reported in one of the salt-water species of the *A. gambiae* complex, namely *A. melas* in Angola.

The operational significance of DDT resistance in *A. gambiae* in the African Region has not been determined in view of the fact that no large scale spraying operations with this insecticide have been implemented.

Dieldrin resistance has been reported in *A. funestus* from several countries in West Africa but records of DDT resistance have not been confirmed. In a few countries a small number survived with one hour exposure to 4% DDT but two hours exposure to this concentration gave a complete kill.

A. nili plays an important role in malaria transmission in some localized areas, in addition to *A. gambiae* and *A. funestus*, and has shown resistance to dieldrin.

In most of the cases insecticide resistance in the above-mentioned vectors has coincided with the application of pesticides in agriculture as, for example, in Upper Volta where organochlorine and other insecticides are used for controlling cotton pests and in Togo where DDT and HCH are being used for controlling cocoa pests.

The American Region. — *A. albimanus* is largely responsible for transmission of malaria in countries of Central America, where the problem of insecticide resistance has hampered the progress of the malaria eradication programmes (Guatemala, Mexico, Honduras and Nicaragua Malaria Programmes, unpublished reports to WHO).

Dieldrin resistance was discovered in this species in El Salvador, Guatemala, Honduras and Nicaragua since the introduction of malaria eradication programmes in 1957/58. A few years later DDT resistance was reported in this vector and the programmes endeavoured to counteract this problem by applying chemotherapeutic measures in addition to DDT house spraying as far as possible on a total coverage basis. However, from 1970/71 onward, the epidemiological situation, together with the increasing level of DDT resistance, necessitated replacement of DDT with propoxur.

In El Salvador, propoxur resistance was reported soon after the application of this insecticide in 1971 for house spraying and subsequently extended its range in this country and was found in Guatemala and Nicaragua. Lately there is some indication of its presence in Honduras.

Investigations carried out in the above-mentioned countries on multi-resistance in *A. albimanus* have indicated that it is firmly correlated with the extensive application of a variety of OP and carbamate insecticides for controlling cotton and rice pests (6).

In Mexico there was an indication of the presence of incipient resistance to DDT in *A. pseudopunctipennis* in 1959 and resistance was shown to be widespread in 1966/67 and recently it has hampered the progress of the control programme as DDT resistance already existed in the other vector, *A. albimanus*, which occurs in some areas.

In the American Region, the population living in areas affected by vector resistance in Guatemala, El Salvador, Honduras, Mexico and Nicaragua totals 77,831,000, i.e., 20% of the total population living in malarious areas.

The Eastern Mediterranean Region. — *A. gambiae* s.l. is the main vector in Ethiopia, Sudan, Somalia, Saudi Arabia, Democratic Yemen and Yemen. Species B of the *A. gambiae* complex has so far been identified from certain areas in the above mentioned countries while species C was additionally reported from a limited area in Ethiopia [Davidson, personal communication, 1969 and was further studied by White (1974)] (7). Dieldrin resistance has been reported for a long time as occurring in this species in Ethiopia and Sudan. The species of the *A. gambiae* complex identified so far in certain areas of Sudan is species B. The first record of DDT resistance came from El-Guneid locality, Sudan in January 1970. It was soon found to be widespread and has created an operational problem for malaria control in the Gezira irrigated area where cotton is regarded as the best cash crop for the country and various pesticides are extensively used for controlling its pests. There was an outbreak of malaria in 1974/75 in the Gezira area. Field entomological observations together with the periodical susceptibility checking have provided evidence that DDT can no longer be effective against *A. gambiae* used to control malaria transmission (Haridi, unpublished report to WHO). This necessitated the introduction of malathion house spraying and supplementing it by larviciding with temephos during the dry season. In Ethiopia, recent tests have shown a significant survival of *A. gambiae* following exposure to 4% DDT for one or two hours. This may indicate suspected cases of resistance, but this is awaiting confirmation.

A. pharoensis is widespread in Egypt, Sudan, Ethiopia and Somalia, and in Egypt it was incriminated as the principal vector of malaria. DDT and dieldrin resistance were reported in 1959-61 and the operational implications of DDT resistance were determined in a control trial conducted during 1960-1963 (8). The appearance of this double resistance was closely correlated with the use of pesticides for controlling cotton pests. No generalized DDT or dieldrin spraying has been adopted for the control of malaria in Egypt, and the programme there depends on anti-larval control together with treatment for malaria cases.

A. sergenti is an important vector of malaria in certain areas of Egypt, Libya, Jordan and Saudi Arabia. Dieldrin resistance was discovered in 1958 in this species in Jordan (Garret-Jones, unpublished report to WHO) where this insecticide was used as a larvicide. Subsequently, DDT oil larviciding replaced dieldrin and since 1967 temephos has been introduced and houses continued to

be sprayed with DDT. Tolerance to DDT has been reported in 1967 and investigations showed that this might be enhanced in the presence of dieldrin resistance. Recently reports of larval susceptibility testing indicated signs of incipient resistance to temephos but this, as well as the DDT tolerance, are being further investigated (Davidson, personal communication 1975). No adverse effects on control operations have been reported as yet.

A. sacharovi is the major vector of malaria in Syria, Northern Iraq and in certain parts of Iran. The presence of DDT resistance in *A. sacharovi* in Syria was confirmed in 1968. This was proved to be hampering control operations and it was decided to replace DDT by dieldrin spraying (8). Two years after the successful elimination of malaria transmission by dieldrin spraying, a very marked resistance to dieldrin was recorded, but the favourable epidemiological situation nullified the implications of this resistance and there were only sporadic foci which were dealt with effectively by various measures. In Iran, DDT resistance in *A. sacharovi* was reported from Izeh area, Khuzestan, Meshkin-Shahr in the north west and Kazeroun area in the south (9). Measures have been undertaken to prevent the spread from the existing resistant foci.

A. hyrcanus occurs in several countries in the Region such as Afghanistan, Iraq and Iran with the type locality being the Caspian Sea in Iran. In the north eastern region of Afghanistan, pronounced DDT resistance was reported in 1969 in this species which is considered as playing a secondary role in malaria transmission (Onori, Nushin, Cullen and Yakubi, unpublished report to WHO).

Based only on epidemiological evidence, *A. pulcherrimus* has been suspected to be acting as a vector in Iraq (10) and it has been reported to be resistant to DDT near Baghdad. Resistance to dieldrin in Saudi Arabia and Syria has been recorded but there has been no evidence of its involvement in malaria transmission in the two countries. This species has recently been incriminated as the main vector of malaria in the north eastern region of Afghanistan and in Afghanistan the exophagic and exophilic behaviour of *A. pulcherrimus* and *A. hyrcanus* coinciding with the people's habit of sleeping outdoors, has created a problem of persistence of transmission. Chemotherapeutic measures together with DDT spraying and the use of *Gambusia* fish have improved the epidemiological situation (Onori et al., unpublished report to WHO). Some tests carried out in Afghanistan indicated the presence of DDT resistance in *A. pulcherrimus* but its extent has not so far been determined.

A. culicifacies is the principal malaria vector in Pakistan and in the Central Eastern and Southern regions of Afghanistan. It also occurs in Baluchistan Province, southern Iran and United Arab Emirates.

In Afghanistan it occurs with *A. stephensi* in the above mentioned regions and indications of resistance in the two species to DDT were obtained during the period of testing in 1965-1967 in areas in the consolidation² phase of malaria eradication.

The problem of DDT resistance became obvious when DDT spraying failed to control malaria outbreaks which occurred in 1970. In limited scale trials malathion has been found to be effective in reducing malaria transmission by the two above-mentioned species (Onori et al., unpublished report to WHO).

In Iran the species was found to be resistant to DDT in Baluchistan Province after 10 years of dieldrin spraying followed by DDT spraying (11). DDT and malathion spraying was alternated between 1967 and 1973. The DDT resistance was found to be high and the density of *A. culicifacies* reached about 500 per shelter. There was also an increase in the annual parasite incidence. The species remained susceptible to dieldrin and malathion.

In Pakistan, *A. culicifacies*, together with *A. stephensi* are the major vectors of malaria in the rural areas. DDT resistance appeared in both vectors in 1963. Despite this, the epidemiological situation showed a favourable trend during DDT house spraying and a large area was shifted into the consolidation phase. Commencing in 1969 a high level of DDT resistance was encountered and DDT spraying could not curtail the epidemic. Attempts to use HCH have led to a temporary reduction in malaria transmission, but the appearance of dieldrin resistance has blunted the effectiveness of this

²The phase of consolidation begins as the active attack on the vector ends. During the consolidation phase residual pockets of transmission located by case findings are eliminated by means of drugs or re-spraying. This phase ends after three years of active surveillance have shown the absence of any new indigenous cases.

Table 1.—Reported insecticide resistance in the commonest malaria vectors up to the end of 1975^a
(quoted from WHO Chronicle, 1975, 20, p. 199 and updated).

Double resistance — DDT & dieldrin (DL)		Dieldrin resistance alone	
Species	Countries	Species	Countries
<i>A. aconitus</i>	Indonesia	<i>A. aquasalis</i>	Brazil, Trinidad, Venezuela
<i>A. albimanus</i> ^b	Costa Rica, Dominican Republic, El Salvador Guatemala, Honduras Nicaragua, Panama	<i>A. barbirostris</i> ^c	Indonesia
<i>A. albitarsis</i>	Colombia	<i>A. farauti</i>	Solomon Islands
<i>A. annularis</i>	India, Bangladesh ^e (DDT), Indonesia ^e (DL)	<i>A. funestus</i>	Cameroon, Ghana Kenya, Nigeria, Upper Volta
<i>A. culicifacies</i>	India, Pakistan, Nepal	<i>A. nili</i>	Ghana
<i>A. fluviatilis</i>	India (DDT), Saudi Arabia (DL)	<i>A. philippinensis</i> ^e	Sabah-Malaysia
<i>A. gambiae</i> sl	Several African countries (DL)	<i>A. minimus flavirostris</i>	Indonesia, Philippines
species A	Cameroon, Dahomey, Guinea, Nigeria, Togo Upper Volta, (DDT/DL)		
species B	Senegal, Sudan (DDT/DL)		
<i>A. melas</i>	Angola (DDT)		
<i>A. hyrcanus</i>	Afghanistan, Turkey	<i>A. sergenti</i>	Jordan
<i>A. labranchiae</i>	Algeria, Morocco (DDT resistance to be confirmed)		
<i>A.l. atroparvus</i>	Romania		
<i>A. maculipennis</i>	Bulgaria, Romania		
<i>maculipennis</i>			
<i>A. maculipennis</i>			
<i>messeae</i>	Romania		
<i>A. pharoensis</i>	Egypt, Sudan ^e		
<i>A. pseudopunctipennis</i>	Mexico		
<i>A. pulcherrimus</i>	Iraq ^e (DDT), Saudi Arabia ^c and Syria ^c (DL) Afghanistan (DDT)		
<i>A. quadrimaculatus</i>	Mexico, USA		
<i>A. sacharovi</i>	Greece, Syria, Turkey ^d		
<i>A. stephensi</i>	Afghanistan, India, Iran, Iraq, Pakistan, Saudi Arabia		
<i>A. subpictus</i>	Indonesia ^e		
<i>A. sundaicus</i>	Indonesia		

DDT resistance alone

Species	Countries
<i>A. nuneztovari</i> ^f	Venezuela
<i>A. sinensis</i> ^g	Ryukyu Islands, Japan

^aBased on WHO documents ("Records of insecticide resistance in *Anopheles*") and on BROWN, A.W.A. and PAL, R. "Insecticide resistance in arthropods", Geneva, World Health Organization, 1971 (Monograph Series no 38) and most recent records received up to 1975.

^bAlso resistant to propoxur, malathion and fenitrothion in El Salvador and Nicaragua to propoxur in Honduras and to malathion in Guatemala.

^cOne unconfirmed record from Thailand indicating DDT resistance (May 1970).

^dResistance to propoxur, fenitrothion and fenthion confirmed; resistance to malathion to be confirmed.

^eVector status unconfirmed.

^fA single record from Tachira in 1961: see also Brown and Pal (reference in footnote (a)).

^gDieldrin resistant but DDT susceptible in Korea, HONG, H.K. *Korean Journal of Entomology*, (1971)

insecticide. Malathion spraying is being planned in areas where *A. culicifacies* and *A. stephensi* are highly resistant to DDT.

A. stephensi as has been mentioned above, exists in association with *A. culicifacies* in Afghanistan, Pakistan and the United Arab Emirates. In the southern regions of Iraq and Iran and the eastern province of Saudi Arabia, it is considered the major vector responsible for malaria transmission. After prolonged control of malaria with DDT spraying, DDT resistance appeared simultaneously in Iran, Iraq and Saudi Arabia in 1955/56. This necessitated the switch from DDT to dieldrin spraying, but marked dieldrin resistance appeared in 1961, the results of which were that all spraying operations were suspended. An outbreak of malaria occurred in southern Iran and southern Iraq and, in view of the observed reversion of DDT resistance towards susceptibility, DDT spraying was reinstituted. Although transmission of malaria was somewhat reduced throughout 1964-1966, outbreaks of malaria occurred during 1967/68 and field observations together with parasitological evidence demonstrated the ineffectiveness of DDT. Subsequently it was replaced by malathion during 1968/69. This brought down the malaria incidence to a low level and in Iraq transmission has been completely interrupted. (Ossi, Hashmi, Iyengar, unpublished report to WHO). In Iran the introduction of malathion spraying together with supplementary measures, e.g., oiling, and an efficient surveillance mechanism in the malaria refractory zone, has led to a reduction in vector density and a decrease in the parasite rate by 30-90% (Tabibzadeh, unpublished report to WHO). However, for organizational reasons, there has recently been some deterioration in the epidemiological situation.

In the Eastern Mediterranean Region, it is estimated that the population in areas affected by vector resistance in Afghanistan, Iran, Iraq, Pakistan and Sudan, totals about 69 million, representing about 51% of the total population of the malarious areas.

The European Region. — Although *A. sacharovi* occurs in a number of countries in the southeastern part of the European Region, its resistance to insecticides has not created much of a problem since malaria transmission has been completely controlled in a large part of the range of *A. sacharovi* and of other members of the *A. maculipennis* group. Malaria has been eradicated except from Turkey where *A. sacharovi* is the main vector in the rural areas. As early as 1958, DDT resistance was recorded in this species in Turkey and soon afterwards dieldrin resistance was also reported in some areas. However, it was only from 1968 on that the problem of dieldrin resistance in addition to that of DDT resistance manifested itself when attempting to control malaria outbreaks in areas in the consolidation phase of the malaria eradication programme (Ramsdale, Talbani, unpublished report to WHO). Malathion replaced DDT spraying but had limited success in view of its unpleasant odour which led to inhabitants refusing to have their houses sprayed. Very recently resistance of this species to propoxur, fenthion and fenitrothion and possibly to malathion has been reported from Adana-Mersin Plains, although in some areas such insecticides have not been used in public health, but a variety of these groups have been applied by aerial spraying for agriculture pest control. Because of the existence of this multi-resistance non-insecticidal measures including a good case detection system with efficient treatment of cases as well as biological control, are required particularly in areas where agriculture development is proceeding rapidly.

Turkey is the only country in the Region where the problem of vector resistance exists and here it covers an area with 3,100,000 population, representing about 9% of the total population of the malarious areas.

The South-East Asia Region. — *A. aconitus* is the main vector of malaria in Indonesia (Arwati, Verdrager and O'Connor, unpublished report to WHO). In 1962/63 DDT resistance was reported in this species in eastern and central Java, but it did not at that time seem to cause any difficulties. However, the level of resistance subsequently increased and studies in 1972 showed that malaria transmission could not be reduced significantly with DDT. A trial with malathion is being planned and attempts to introduce environmental control measures are being investigated.

A. culicifacies is the principal vector of malaria in the rural areas of India and Sri Lanka and it has shown pronounced DDT resistance in the former country since 1957. Despite this, the national eradication programme succeeded in interrupting malaria transmission and shifting large areas into the consolidation and maintenance phase. It was only from 1966/67 on that the DDT resistance problem became apparent when DDT and HCH failed to control malaria outbreaks. Malathion spraying has given satisfactory results (Pattanayak, Rajagopal, unpublished report to WHO), although first cases of resistance to malathion have been reported from Gujarat and Maharashtra.

In Sri Lanka the first report of DDT resistance came from the areas in the consolidation phase of malaria eradication in 1968 and subsequently DDT spraying to control malaria epidemics has not given satisfactory results. Malathion is being sprayed in certain epidemiologically important areas while different regimens of DDT spraying are being applied in other areas. Attempts are being made to provide funds to replace DDT with malathion (Abeyesundere, Herath, Clarke and Wickremasinghe, unpublished report to WHO).

A. stephensi is a major vector in the urban areas in India and it has shown resistance to DDT and dieldrin but interruption of malaria is being attempted by antilarval measures in addition to chemotherapy. It is estimated that the population in areas affected with the problem of vector resistance in the South-East Asia Region is about 176,345,000 of the three above-mentioned countries, representing 26% of the total population of the malarious areas.

The Western Pacific Region. — Although dieldrin resistance in *A. farauti* Solomon Islands, *A. minimus flavirostris* Philippines, and *A. sundaicus* Sabah, Malaysia, were reported, no problems have been created to the malaria programmes since the earlier dieldrin spraying system was suspended and replaced by DDT. On the other hand, *A. sinensis* in Korea which is highly resistant to dieldrin, has remained susceptible to DDT but has now shown resistance to fenitrothion and fenthion. Again there have been no operational problems arising from this resistance.

Part 2: Other Vectors of Disease

The Present Status

Culicine Mosquitos. — *Aedes aegypti*. — The resistance situation of *Aedes aegypti* does not seem to have changed substantially in the past six years. There is widespread resistance to organochlorine insecticides (especially DDT) in most tropical countries which has, for about a decade, stimulated a search for suitable alternatives. Certain organophosphorus compounds of very low mammalian toxicity (e.g., temephos) have been quite widely used and, so far, no confirmed case of resistance has been reported.

There are two regions where the problems of *A. aegypti* resistance and the need for alternative insecticides are of special interest. In the Americas, a protracted attempt to eradicate the species from the Western Hemisphere has inevitably resulted in increased resistance (see Table 2). In Southeast Asia, throughout the past decade, there has been a continuing threat of haemorrhagic dengue, which is largely transmitted by *A. aegypti*. In view of widespread resistance to chlorinated hydrocarbon insecticides their use for the control of *A. aegypti* would be out of question. There are two options in the strategy of control of this mosquito: (a) by larviciding in the long-term control as a preventive method and (b) by adulticiding as the emergency method for control of epidemics by ULV application of pesticides.

Culex pipiens fatigans. — Replies to the current survey frequently repeated the observations of resistance to organochlorine insecticides, which has been widespread since about 1960. In many parts of Southeast Asia, organophosphorus larvicides have been used against the mosquito in urban regions, for some five to ten years, apparently without producing resistance. In California treatments of organophosphorus larvicides have been made against this mosquito because of the nuisance of its bites. This has resulted in multiple resistance to a range of OP insecticides at low but significant levels.

There have been isolated reports of malathion- and diazinon-resistance in *C. p. fatigans* from other areas. An early record was that of Mouchet (1960) (12) from the Cameroons; but in a later publication, Mouchet (1968) (13) noted that there had been no further information on this point and that the situation was normal. In the WHO computer print-out records, there are scattered records of rather high LC_{50} values for larval tests with malathion from the Kyukyu Islands (November 1967) and Okinawa (May 1965).

It is possible that these isolated cases did not develop to well-established problems because of limited usage of the OP compounds. It is fairly evident that such resistance can develop (as seen in California) and also as a result of laboratory selection, which has been able to produce resistance levels up to 10 x for fenthion (Tadano and Brown, 1966) (14) and rather lower levels to other organophosphates (Ziv et al. 1969) (15). Also, laboratory selection has induced carbamate resistance up to a level of 25 x (Georghiou et al. 1966) (16).

Nuisance Mosquitos and Virus Vectors. — Although some anopheline mosquitos may be considered a nuisance from their bites, the main cause of annoyance is from various culicine species,

Table 2.—Current status of *Aedes aegypti* control schemes in the neotropics and checks of resistance status (Data supplied by PAHO, 1974).

Territory	Control schemes		Resistance (S or C) (2)					
	Insecticide	Scale (1)	DDT	HCH diel	Mal.	fenth	Abate	Durs.
Anguilla	fenthion, Abate	S	C	C	S	S	No	No
Antigua	fenthion, Abate	M	C	C				
Aruba	Malathion	M	C	C	No			
Bahama I.	none	—	C	C	S	No	S	No
Barbados	fenthion, Abate	L	C	C	No	S		
Brazil		L	C	C	No	No		
Brit. Virgin I.	fenthion, Abate	S	C	C		S	S	
Cayman I.	Abate	S	C	C				
Colombia		L	C	C	No	No	No	No
Costa Rica		M	C	C	S	S		No
Cuba		L	C	C	S	S		
Curacao	Malathion	M	C	C	No	No		
Dominica	none	—	C	C	S	S	No	
Dominican Rep.	none	—	C	C	No	No	No	
El Salvador	DDT	S	C	C				
Fr. Guiana		M	C	C	No	No	No	No
Grenada	fenthion	M	C	C		S		
Grenadines	none	—	C	C	No			
Guadeloupe	Malathion	M	C	C				
Guatemala	fenthion, Abate	M	C		No	No	No	
Guyana	fenthion, Abate	L	C	C				
Honduras	fenthion, Abate	M	C	C	No		No	No
Jamaica	Abate	S	C	C	No	No	No	
Martinique	Malathion	M	C	C	No	No	S	
Montserrat		S	C	C	S	S		
Nevis		S	C	C				
Panama	Malathion, Abate	M	C	C	No		No	No
Saba		S	C	C				
St. Eustatius		S	C	C	No		No	
St. Kitts	none	—	C	C	S	No		
St. Lucia	none	—	C	C	No	S	S	
St. Martin			C	C	S		No	
St. Vincent			C	C	S		S	
Surinam	fenthion, Abate	M	C	C	No		No	
Trinidad	fenthion	—	C	C				

(1) S = small; M = medium; L = large. (2) S = suspected; C = confirmed.

which propagate in vast numbers and generally bite out of doors. In some cases, these may be involved in the transmission of certain encephalitis viruses between different warm-blooded animals and, occasionally, to man.

The resistance situation regarding nuisance culicines of North America was outlined in the previous survey. Since then, there has been further deterioration. Thus, resistance in the Californian species (especially *Culex tarsalis*) has gradually extended to all types of organic insecticide (including, apparently, some insect development inhibitors).

Sandflies (Phlebotomus). — No further information has been received in regard to sandflies or the diseases (leishmaniasis) transmitted by them. It is presumed that no case of resistance has developed.

Blackflies (*Simulium*). — Species of *Simulium* were relatively slow to develop resistance, possibly because they had not been subjected to the intensity of selection which was applied to other insects of medical importance. In the 1968 survey *S. aokii* had been found resistant to organochlorines in Japan and *S. venustum* in Canada. The latter was confirmed in the present questionnaire; and a further example was quoted of DDT-resistant *S. bainanae* in a report from the Philippines.

Of rather more importance, however, is the record of suspected DDT-resistance in the African onchocerciasis vector, *S. damnosum* in south-west Upper Volta and also in the northern Ivory Coast.

Tsetse flies (*Glossina*). — Insecticidal attack on tsetse flies is tending to increase. Only one questionnaire mentions them, however, recording moderate to large control schemes with DDT, endosulfan and dieldrin. No report of resistance has been received.

Houseflies (*Musca domestica*). — Resistance in houseflies continues to be widespread, with some evidence of increasing involvement of the organophosphorus compounds. Thus, in the previous (1968) survey, 37 replies mentioned fly resistance and 13 of them (35%) involved phosphorus insecticides. In the present inquiry only 22 replies mentioned fly resistance, but 17 of them (80%) involved phosphorus compounds. As before, there was a suggestion of association with probable usage: organophosphorus resistance was more common in North America than in South America, and more in Western Europe than Eastern Europe.

Lice (*Pediculus humanus*). — *Pediculus humanus humanus*. — Since the two WHO sponsored surveys of susceptibility levels in body lice (1957 and 1963) no further extensive survey has been made; but the subject was discussed at a PAHO/WHO Symposium on the Control of Lice and Louse-Borne Diseases (December 1972). At least in two areas (Yugoslavia, South Africa) DDT powder had been successfully used in recent years, despite evidence of DDT resistance. In Hungary, malathion was being used, owing to the banning of DDT (apparently on toxicological-environmental grounds).

Most significant was the record of malathion resistance in Burundi (Central Africa) where the powder was used in 1969 to combat a typhus epidemic. Malathion was used because of evidence of DDT-resistance in local body lice (though this was not universal). Unfortunately, the lice were soon found to be malathion resistant in one area, apparently because of the extensive use of this insecticide to control pests of coffee (Miller et al. 1972) (17). Malathion resistance in lice has also been recently reported in Ethiopia (Sholdt 1976, personal communication).

Pediculus humanus capitis. — In the 1968 survey a suspected resistance of head lice to organochlorine insecticides in England was mentioned. This has been amply confirmed and as a result of further research a malathion-based insecticide has been introduced and is now being widely used (Maunder 1971) (18). In the current survey, DDT-resistance in head lice is reported from Denmark, Hungary, and South Africa, while suspected cases of resistance to lindane has been observed in Canada and the United States of America. Confirmation of resistance is not easy, because the WHO standardized method for body lice is not feasible with the more delicate head lice, which tend to die in the controls.

Malathion (of great purity to avoid odour) has several advantages over the organochlorine insecticides. It is quicker in action and is rapidly metabolized in the body, so that there is no possibility of adding to insecticide traces in body fat (for which reason organochlorines have been banned in several countries).

Fleas (*Xenopsylla*). — A few more scattered reports of resistance to organochlorine insecticides have been made, but there is no evidence to date of resistance to organophosphorus insecticides and the situation appears substantially the same as in 1968.

Reduviid bugs (*Rhodnius*, *Triatoma*, *Panstrongylus*). — The first definite evidence of insecticide resistance in a vector of Chagas' disease came from Venezuela in 1969. Strains of *Rhodnius prolixus* from Trujillo State were found to be abnormally resistant to the dieldrin/HCH group; this was 10 years after the initiation of an anti-Chagas dieldrin spraying campaign in the country. The most recent information indicates that *Triatoma maculata* has developed the same type of resistance, also in Venezuela.

Acarina (ticks and mites). — As in the 1968 survey, virtually none of the recent replies made any reference to ticks or mites. The main usage of acaricides against tick vectors of human disease seems to be in Eastern Europe, against ixodids which transmit viral diseases (e.g., Russian spring-summer encephalitis). Susceptibility tests against adults of such ticks have been extensively undertaken by Russian and Czech workers. There are however, no reports of resistance.

Resistance in cattle ticks (especially *Boophilus microplus*, in Australia) is, of course, a well known serious veterinary problem. The Food and Agriculture Organization is known to be considering the possibility of a world survey of such ticks to assess the status of resistance in different countries.

Bed bugs (*Cimex*). – Bed bug resistance to organochlorines was mentioned in numerous replies and the problem has certainly not improved since 1968. In England, for example, DDT- and HCH-resistance was first definitely confirmed in 1974. The impact of organochlorine resistance may be less evident because these chemicals are being abandoned in some countries on grounds of possible environmental hazard. No additional example of malathion resistance was mentioned in the answers to the questionnaire, except resistance of *Cimex hemipterus* to malathion in Maharashtra State (VBC/IRG/75.29 item 10).

Cockroaches (*Blatella germanica*). – Cockroach resistance was seldom mentioned in replies to the questionnaire; but it is known that organochlorine resistance is widespread in *B. germanica* (Brown and Pal 1971) (19). In the United States of America, malathion resistance has been confirmed and various other forms of resistance to organophosphorus and carbamate insecticides are known.

Measures to Counteract Vector Resistance to Insecticides

Malaria

The setbacks which occurred in malaria programmes due to vector resistance to insecticides, add still more dimensions to the already existing financial, administrative and operational problems and have made the future prospects for successful control of malaria not very bright.

In order to deal with the present epidemiological situation and to prevent its further deterioration in countries affected by anopheline vector resistance where recent malaria outbreaks have occurred, there is a need:

(i) to provide financial resources for procuring the appropriate insecticides. Spraying operations should be supported by an efficient mechanism for the detection and treatment of malaria cases. Even if financial constraints could be solved and new effective compounds could be made available, malaria control concept and strategy with no time limit and based mainly on the use of chemicals which will produce resistance sooner or later, will not be able to achieve any major impact on communicable diseases including malaria. Some serious innovative thinking has to be made to review the policy and strategy of vector-borne diseases including malaria.

(ii) to develop new groups of biodegradable insecticides. The operational life of these insecticides should be subjected to thorough laboratory and field investigations.

(iii) to establish close cooperation between public health and agricultural authorities to control the indiscriminate use of pesticides.

(iv) to develop other measures of control such as biological and genetic methods for controlling the vector.

(v) to assist developing countries in implementing engineering methods as permanent mosquito control measures particularly in development schemes where water management and species sanitation can effectively control breeding of mosquitos. As such the measures are likely to be cheaper and safer than insecticides in the long run.

(vi) laboratory and field research programmes should be encouraged and further stimulated; particularly studies on population dynamics of anopheline vector species and the factors influencing the speed of selection for resistance as well as cross-resistance patterns, and their impact on disease prevalence.

Other Diseases

The above considerations would also apply to the control of other vector-borne diseases. The recent WHO Expert Committee has summed up as follows:

“The Vector Control policy to counteract resistance should be based on reducing the intensity of chemical selection as much as possible by (a) reducing either the frequency of pesticide applications or their persistence and coverage to the minimum need for disease control (b) reducing as far as possible agricultural use of every persistent chemicals and (c) supplementing chemical control by alternative methods wherever feasible”.

A summary of the WHO Expert Committee report on Resistance of Vectors and Reservoirs of Disease to Pesticides is given in Annex I.

Acknowledgment

Full acknowledgment is made with grateful thanks to the National and WHO staff for the information which they contributed as indicated in the text of this review. Thanks are also extended to all those who have submitted the results of susceptibility tests carried out on a wide range of vectors in many countries on the basis of which the information contained in this paper has been updated.

Annex I

In view of the fact that insecticide resistance is probably the biggest single obstacle in the struggle against vector-borne diseases, particularly malaria, the Expert Committee was requested to review the problem in depth and advise WHO on the most hopeful and realistic future policies for vector control.

The report of the Committee discusses the present status of resistance in mosquitos and other insects of medical or veterinary importance to the main insecticides in use and also to insect development inhibitors, chemosterilants, and microbial control agents. Resistance to pesticides in reservoirs and intermediate hosts of disease is also considered. The countries from which insecticide resistance has been reported are tabulated for over 120 species of insect and data are given for selected countries in four of the WHO Regions concerning the proportion of the population in the malarious areas that live in places where insecticide resistance is an operational problem. In the WHO Eastern Mediterranean Region these proportions vary from 7%-85% according to country and the average for the selected countries is 29% of the population.

In reviewing the principles of the WHO standard procedures for measuring insecticide resistance the Committee decided that greater use could be made of diagnostic doses or concentrations of insecticides. The modifications required to the standard tests for this and other technical reasons are fully described in the report.

The genetic and biochemical bases for resistance are discussed in relation to the development of cross-resistance and to ways of delaying the appearance of resistance in the field. This is followed by a discussion of the use of alternative chemicals, in particular those with a different type of chemical structure or a novel mode of action.

The importance of the insecticide resistance problem and its impact on the control of vectors and reservoirs of disease are problems encountered so far are considered at length in the report, the effects on malaria control programmes being reviewed separately for each of the WHO Regions.

As regards future vector control policies, the report says that the object should be to counteract or delay the development of resistance mainly by alteration of the type, or reduction of the degree, of selection pressure. This should be achieved by reducing either the frequency, the coverage, or the persistence of insecticide applications by reducing as far as possible agricultural use of persistent chemicals, and by supplementing chemical control by alternative methods whenever feasible.

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Pesticide Management on a Major Crop with Severe Resistance Problems

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ABSTRACT

During the late 1960's, cotton cultivation in Nicaragua reached a disaster phase originating mainly in the high resistance that some of the key pests developed to insecticides. The economical and ecological impact of the excessive pesticide use is discussed as well as the steps taken to overcome the difficulties associated with resistance, through the implementation of the philosophy and practice of integrated pest control. Emphasis is placed on the importance of continuous monitoring of insecticide resistance in Central America, particularly on those species which migrate into the cotton regions of the United States.

The growing and marketing of cotton is the most important economic activity in Nicaragua. As a cash crop it contributes more than 20% of the total exchange earnings of the country (CONAL 1972). With the introduction of synthetic organic insecticides in the 1950's the commercial cultivation of cotton became possible; within a short period of ten years cotton production was intensively developed, thus promoting the mechanization and modernization of the agricultural sector generally (Belli 1968).

Apart from some failures experienced during the late 1950's, mainly due to climatic and marketing factors, cotton cultivation flourished, contributing substantially to the economic growth of the country, and reached its peak in 1965. But in the next five years the situation reached a crisis (Falcon 1971). Production decreased at an annual rate of 15.9% (CONAL 1972) and the country came very close to bankruptcy. The primary cause of this situation was the failure to achieve control of the pests by the prevalent unilateral reliance on chemical pesticides. Problems of serious and increasing resistance to insecticides were evident (Smith 1969, Peterson et al. 1969). The explosive populations of *Heliothis zea* (Boddie) and *Spodoptera sunia* became difficult if not impossible to control. The whitefly, *Bemisia tabaci* (Gennadius), became increasingly tolerant to the mixture of toxaphene-DDT-methyl parathion in common use (Kraemer 1966). As it is usual under these circumstances the growers challenged the resistance of the pests by simply applying the pesticides at higher dosages and at closer intervals (Brown 1974). An average of 25-30 treatments per season were made, with extreme individual cases of over 48-50 applications per season in single fields (Lipes 1966, Smith 1969). During the 1966-67 season the cotton fields of Nicaragua were blanketed with an average of 99.2 liters of liquid insecticide and 18.7 kilograms of dust formulations per hectare (Smith and Reynolds 1968).

Too many different pesticides and combinations of pesticides were available in the local market, to the point that the farmer simply did not know which pesticide to select out of more than 75 different possibilities (E. Somarriba et al. 1968). On many occasions mixtures of 5 different insecticides were employed in a single application. Worst of all, new pesticides not even approved for use in their countries of origin were introduced without restriction and were applied in the cotton fields at a commercial level at the expense and risk of growers (E. Somarriba, et al. 1968), who paid the high cost of field trials that otherwise should be charged to the manufacturers. That was the golden era for the pesticide companies which provided well remunerated technical agents to explain the pesticide failures, recommend new formulas and combinations and sell more and more products.

That was not all. Severe changes in the pest complex occurred. Although the false pink bollworm, *Sacadodes pyradis* Dyar, which was a primary pest in the 1950's practically disappeared, and the boll weevil, *Anthonomus grandis* Boheman, eventually became a pest. On the other hand, the prompt resurgence of primary pests was a common phenomenon and insects of secondary importance like the beet armyworm, *Spodoptera exigua* (Hübner), the cabbage looper, *Trichoplusia ni* (Hübner), and the plant bugs, *Creontiades* spp., became considerable pests due to their abundance and high levels of damage.

Beyond the cotton fields the situation in Central America was even more dramatic. Thousands of insecticide poisonings and hundreds of human deaths occurred (van den Bosch 1972); the highest contamination in the world of DDT and BHC residues in mother's milk was recorded (Olszina-Marzys et al. 1973), and the cases of malaria increased in the northwestern Pacific plains of Nicaragua as a result of the high insecticide resistance developed by its vector, *Anopheles albimanus* Weidemann, associated with the intensive use of pesticides in cotton growing areas (Georghiou 1972, Georghiou et al. 1973).

It was fortunate for Nicaragua and the rest of Central America that the crisis did not reach the extreme that occurred in the Matamoros-Reynosa and Tampico-Mante areas of northeastern Mexico and the Lower Rio Grande Valley of Texas (Adkisson 1971). Both cases presented much similarities but in Central America the problem of insecticide resistance was mainly associated with the bollworm, *Heliothis zea* Boddie, that seems to be less consistent than the resistance affecting the populations of the tobacco budworm, *H. virescens* (F.) in Mexico and Texas. Evaluations made by Wolfenbarger et al. (1971, 1973) indicated that *H. zea* from Leon, Nicaragua, was 44 times more resistant to methyl parathion than strains of the same species from Brownsville, Texas, and 23 times more resistant to endrin than *H. zea* from Stoneville, Mississippi.

Against this background, the situation became so difficult that a revision of the methods of insect control had to be done and an integrated pest management approach was considered with the guidance of the school of integrated pest control from the University of California.

Since 1970 the practice of integrated control of cotton pests has been very actively implemented in Nicaragua with the technical advice of FAO, and problems deriving from the resistance to insecticides have been largely overcome by means of the following countermeasures:

1. Discontinuation of the use of endrin for the control of the highly resistant *H. zea* and *Spodoptera sunia*.

2. Revision of the economic population threshold for these pests. The economic threshold demanding treatment for bollworms control was raised from 8-10 to 25-30 larvae per 100 plants (E. Somarriba 1972). It was also demonstrated that cotton plants up to 75 days old can tolerate 50% foliage damage (A. Somarriba 1972), and 100% fruiting-parts injuries (Vaughan and Esquivel 1975) without significant reductions in yield.

3. Full advantage has been taken of the action of natural enemies since they are the most important regulating factors of pest populations during the early season. Mass releases of *Trichogramma* for the control of *Alabama argillacea* and *H. zea* are made to complement the action of natural enemies during that period.

4. The interaction between the *Spodoptera sunia* populations with its alternative host plants and its natural enemies is monitored to provide a background of knowledge for the regulation of this pest (Vaughan 1975).

5. Pesticide treatments are based on active scouting and monitoring of the pest complex and crop damage, beneficial organisms, and plant growth and fruiting pattern. The phenology and pest population dynamics are also considered for guiding measures of control at zonal level throughout the extension programme of the National Bank of Nicaragua.

6. It has been proved (E. Somarriba et al. 1968, Carcache and Salazar 1974) that the dosage and frequency of insecticide applications can be substantially reduced with no significant effects on yield. The cotton statistics themselves have shown that after a certain number of treatments the yield decreases as much as the number of applications increases (CONAL 1975).

7. Since it is recognized that the explosive populations of *Heliothis* and *Spodoptera* are chemically induced, treatments are delayed as long as possible during the first half part of the season.

8. The use of partially selective insecticides, especially trichlorfon, chlordimeform and commercial preparations of *Bacillus thuringiensis* Berliner, has been increased.

9. Cultural control practices have been emphasized, particularly the management of crop residues, the rational use of nitrogen fertilizers, the regulation of planting dates, dense seeding, timely

and selective thinning, defoliation, early harvesting and use of crop traps before the normal growing season for the preventive control of the boll weevil.

All these aspects and other practices of pest management have determined a more effective control of the pests, a substantial reduction in the number of insecticide treatments, a greater stability in cotton production, a more profitable crop and less deterioration of the general environment. Even so, complete success has not been achieved and problems still remain to be solved. The boll weevil has taken again its place as the first pest of cotton in Nicaragua and alternative methods for its control are under study. The false pink bollworm populations have reappeared. The strong influence of the pesticide companies has not declined to the extent that is convenient and desirable.

Studies on insecticide resistance are not being given proper attention, and reports in this respect have been based mainly on failures of control (Fuente 1971). For Central America, the constant monitoring of resistance is of critical importance in order to avoid all the economic and ecological detrimental consequences that has been experienced in the past. Moreover these studies have acquired international importance since regions of the United States are subject to the immigration of possible resistant strains from the southern countries of America (Wolfenbarger et al. 1973). An international interest and coordinated actions in this sense seem to be of priority importance.

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Epilogue: Resistance as a Factor in Pesticide Management

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Now that we have been told that we have induced pesticide-resistance in some 300 species of arthropods only 30 years after the introduction of the synthetic organics, it is time to take stock of our accomplishment. The accomplishment is, not only substituting new genotypes that had never succeeded under natural conditions, but also perpetuating resistant strains which, like those of the multiresistant *Heliothis virescens*, are notoriously ill-adapted and much harder to colonize than the normal strains. Yet if we relieve the insecticide pressure and let the resistance genotypes become rare again, there persists a changed background of residual inheritance in the genome that makes the strain regain its resistance as soon as the insecticide is reapplied. For example, Danish houseflies recovered in 2 months the DDT-resistance or cyclodiene-resistance that it had taken them 5 years to lose and 2 years to develop in the first place. Thus our accomplishment has a certain permanence.

Also relatively fixed is the arsenal of our weapons against insect pests. Classified according to the resistance types that they induce, there are only 6 groups, two of which contain the organochlorines just mentioned, plus the organophosphates, carbamates, pyrethroids and formamidines. To develop and clear a new insecticide in the U.S.A. and put it into general use takes at least 7 years and costs a figure quoted at \$7.5 million two years ago (Wecksler et al. 1975) and which is more than \$10 million now. Small wonder that Dow Chemical was reluctant to develop chlorpyrifos (Dursban) a decade ago, that Monsanto gave up its development of aniline derivatives as insecticides (Darlington et al. 1972, Cantu and Wolfenbarger 1973) and turned its full attention to herbicides which are simpler and easier to clear, and that Phillips-Duphar came to the most promising IGR diflubenzurone (Dimilin) as a by-product of its research on urea herbicides. Having reached a situation where registrations of new insecticides are counterbalanced by suspensions, with yet others to be asked to justify their existence, we must make do with what we've got, or rather with what we'll be left with.

The time frame of the resistance problem in terms of the number of species involved (Fig. 1) shows that the two types of organochlorine-resistance were developed usually in about 10 years, the cyclodienes encountering it somewhat faster than the DDT group. Resistance to organophosphorus compounds comes to fruition usually 10 years after that, with carbamate-resistance taking the same time but working a little faster when it builds on a base of OP-resistance. The successive resistance types more often develop in the one-and-the-same species than in new ones, so the horizontal lines on the graph often indicate the road of a given pest in overcoming the succession of weapons used against it. Thus pests like *Heliothis* and *Spodoptera* caterpillars, *Aedes nigramaculis* mosquitos, houseflies, Tetranychid mites and cattle ticks, having come up with 4 or 5 resistances, have almost won the war against the chemists, while species like the cabbage looper and the western corn rootworm are approaching that condition. At present there are only 4 examples of pyrethroid-resistance extant, which have recently been joined by 2 cases of formamidine-resistance, both in orchard mites, and the new insect growth regulators have a clean sheet in the field. Yet there is a danger that we will allow these weapons too to be blunted, and we must ask ourselves what we would do now to avoid our sorry record of the past 30 years.

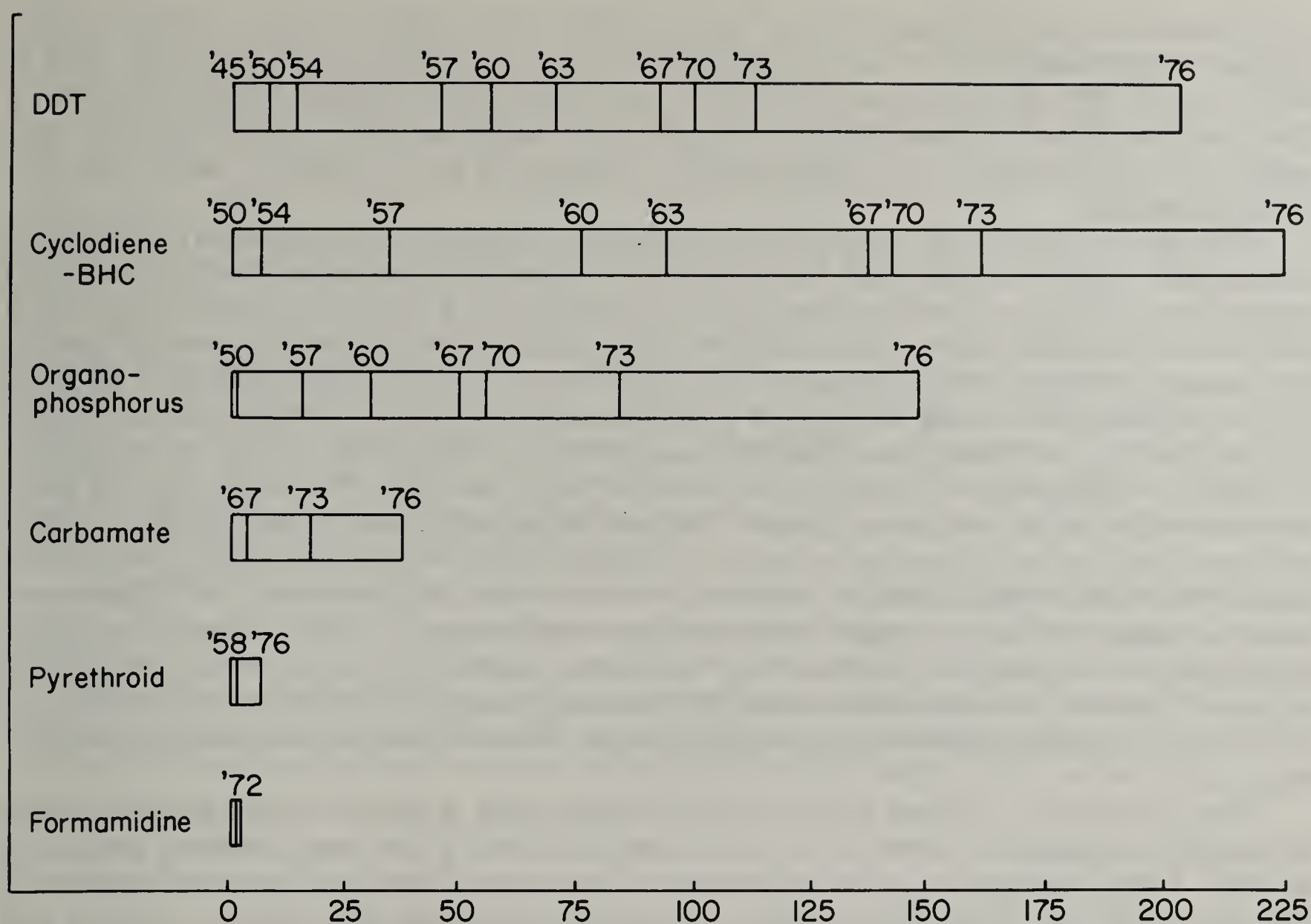


Fig. 1. —Time-scale of development of resistance to the main groups of insecticides (from Metcalf 1955, Brown 1951, 1958, 1961, 1963, 1968, 1971, Georgiou 1976).

Table 1.—Failure of certain insect species to develop resistance to certain insecticides.

Species	Insecticide	Locality	Date in Field	Gen'ns in Laboratory	Reference
<i>Pyrausta nubilalis</i> (European corn borer)	DDT	N. America	1950-65	—	Brown 1971
<i>Aonidiella aurantii</i> (California red scale)	Parathion	California	1951-63	34	Cressman 1963
<i>Diatraea saccharalis</i> (Sugarcane borer)	Azinphosmethyl	Louisiana	1964-72	6	Reagan et al. 1973
<i>Anthonomus grandis</i> (Boll weevil)	Malathion	W. Texas	1963-72	—	Bottrell et al. 1973
<i>Choristoneura occidentalis</i> (Western spruce budworm)	Mexacarbate	Idaho	—	14	Robertson & Lyon 1973
<i>Diabrotica virgifera</i> (Western corn rootworm)	Diazinon	Nebraska	1963-73	—	Ball 1973
<i>Culex quinquefasciatus</i> (Southern house mosquito)	Flit-Mlo	Texas	—	60	Micks & Gaddy 1973

Occasionally, nature comes up with the unexpected, and resistance does not develop. As a collector's item (Table 1), here are some examples of long-term selection pressure having failed to induce, as with DDT in the European corn borer, any development of resistance. But one must now expect any insecticide to induce resistance to itself in any target pest. We can learn quite a lot from applying laboratory selection to colonized strains, although we will not learn the worst that could happen in the field.

With the mosquito *Culex pipiens* and its subspecies *fatigans* (*quinquefasciatus*), strains have been obtained which previously had the minimum of exposure to insecticides, and compounds in different chemical groups have been compared for the speed with which they induce resistance in these strains. On *Culex fatigans*, selection with organochlorines in each generation would raise the LC_{50} about 100 times in 10 generations, whereas the OP's and carbamates would increase it about 10 times in 20 generations. Among the group of compounds known as juvenile-hormone mimics, triprene increased the LC_{50} of *Culex pipiens* larvae 10 times in 20 generations, while methoprene increased it 80 times in 34 generations of selection. On the other hand, two other JH mimics made the larvae more susceptible rather than more resistant. The urea derivative diflubenzurone induced a 5-8-fold resistance during the first 10 generations when the mosquito larvae were selected (Fig. 2). In a normal strain of the flour beetle *Tribolium confusum*, selection with diflubenzurone for 8 generations induced a degree of tolerance, while the Zoecon compounds induced a 4-7-fold resistance not only in the flour beetle but also in the milkweed bug *Oncopeltus fasciatus* (Fig. 3). So, as has been found in the housefly and the mosquito *Culex tarsalis*, the promising group of compounds known as IGR's are just as prone to resistance problems as the organophosphorus and carbamate insecticides at present in use.

The production of resistant strains in the laboratory gives us material with which we can look for remedial compounds to substitute for the original insecticide if and when resistance develops in the field. A full investigation of the cross-resistance spectrum of the strain, performed after it has been selected for 10, or for 20 generations, will yield the necessary information to make a wise

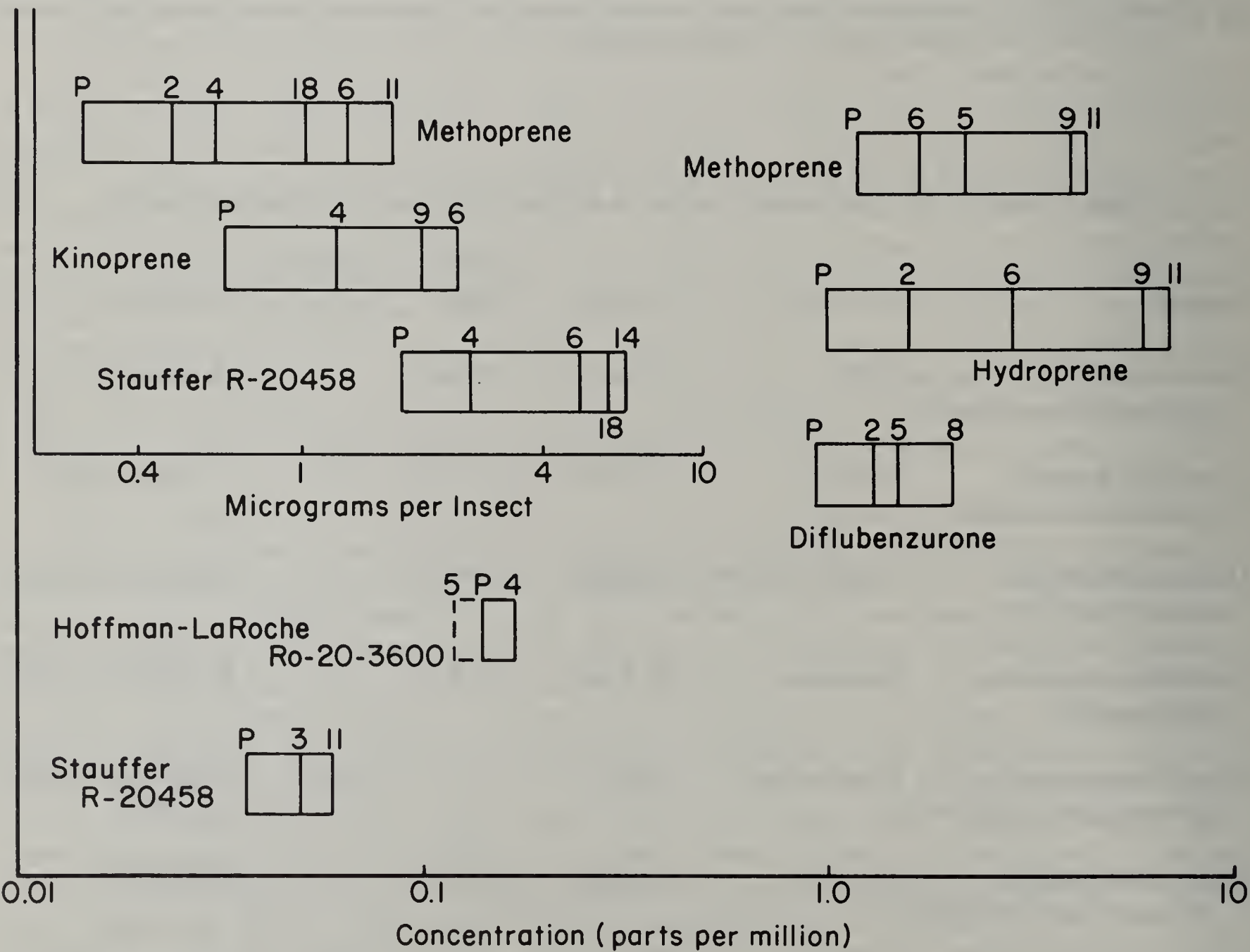


Fig. 2. - LC_{50} levels of successive generations of *Culex pipiens* larvae selected with insect growth regulators.

choice. Although one must have reservations about the validity of laboratory strains to give a complete indication of the potentialities of field populations, they provide the only means to this end until the field populations have reached the stage that the laboratory strains are employed to predict.

Replacements of insecticides for strains which had developed a specific resistance have been quite intensively investigated in mosquito larvae. Fenthion and temephos (Abate) were among the most effective organophosphorus compounds for a purely DDT-resistant strain of *Aedes aegypti* from Trinidad (Table 2), and they are now employed respectively for perifocal and larvicidal control of this important vector species. A susceptible strain of the tropical house mosquito *Culex fatigans* made resistant to fenthion by laboratory selection lost much of its susceptibility to malathion and some to Abate, but there was no cross-resistance to methyl parathion. Vice versa, populations of the malaria mosquito *Anopheles albimanus* in the cotton-growing areas of El Salvador sprayed with methyl parathion, besides parathion, malathion and 2 other compounds (Georghiou 1972), developed strong resistance to the three compounds mentioned but negligible cross-resistance to fenthion. The explanation for this cross-resistance spectrum was provided by Ayad and Georghiou (1975) who found that the cholinesterase of these *albimanus* larvae was highly resistant to paraoxon but remained virtually unchanged in its susceptibility to fenoxon.

Of course, the nature of the remedial insecticide will be dictated by the resistance mechanism that has been developed. Just as there are several mechanisms of DDT-resistance (dehydrochlorination, oxidation, etc.) so there are several mechanisms for OP-resistance including hydrolysis and desalkylation as well as oxidation, reduced penetration and insensitive ChE. The role of the insect toxicologist is to identify the mechanism or mechanisms in the resistant population, and of the geneticist to determine the gene or genes responsible. When the mechanism is enzymic, an enzyme

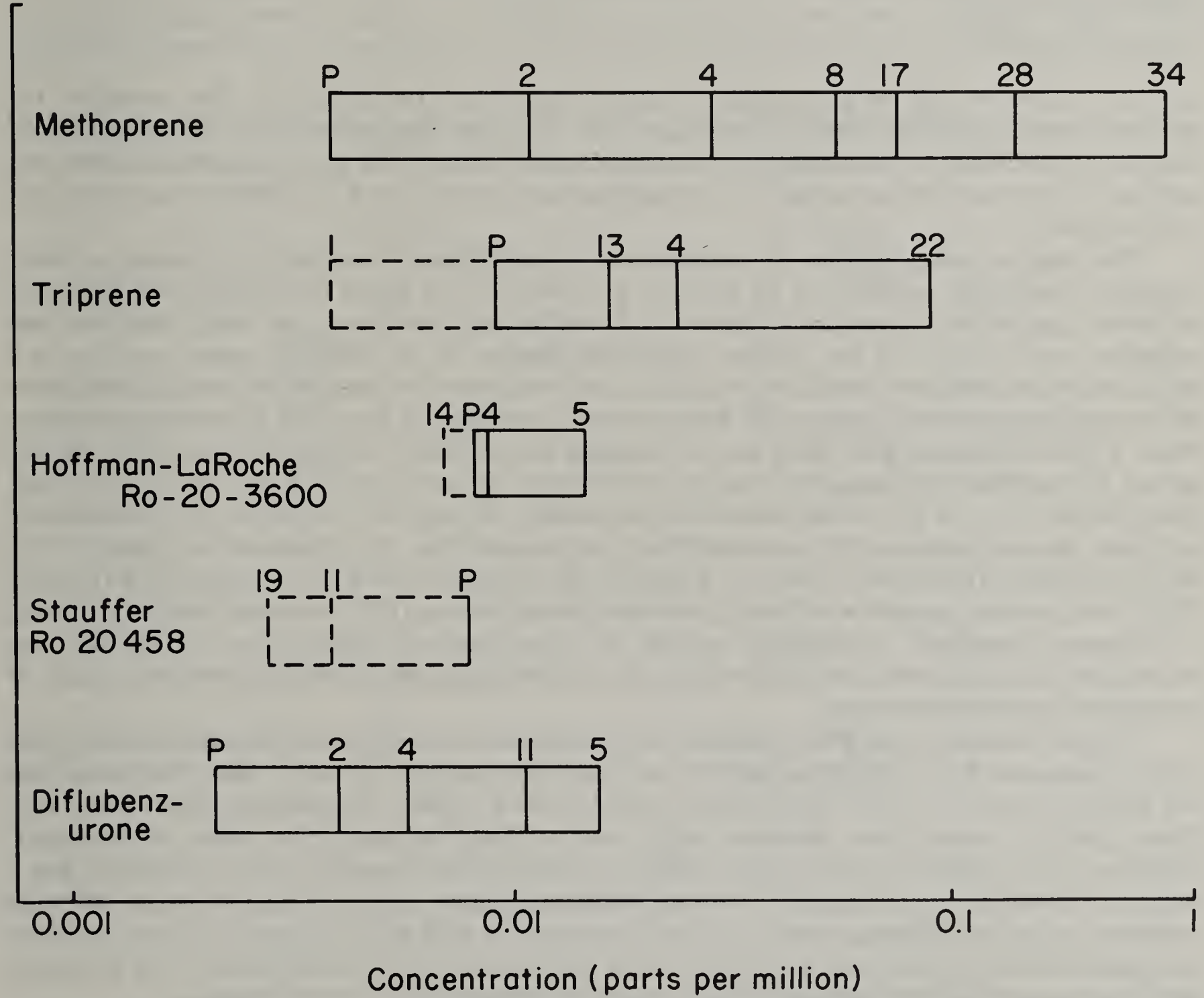


Fig. 3. $-LC_{50}$ levels of successive generations of *Tribolium confusum* larvae, and (upper left inset) nymphs of *Oncopeltus fasciatus*, selected with insect growth regulators.

Table 2.—LC₅₀ levels (ppm) and resistance ratios in laboratory-selected normal strains and a field-selected population.

	<i>Aedes aegypti</i> ¹ DDT-selected LC ₅₀	<i>Culex fatigans</i> ² Fenthion-selected Res. Ratio	<i>Anopheles albimanus</i> ³ Field pop'n, El Salvador LC ₅₀	Res. Ratio
Malathion	0.25	3.6	1.1	12.9
Parathion	0.014	6.0	0.057	18.4
Methyl Parathion	0.0066	1.1	0.17	26.2
Fenitrothion	0.015	—	0.23	9.2
Fenthion	0.020	7.5	0.028	1.2
Chlorpyrifos	—	—	0.015	2.4
Abate (temephos)	0.021	1.8	0.006	1.2

¹ Klassen et al. 1965
² Tadano & Brown 1966
³ Georgiou et al. 1972

inhibitor might be used as a synergist to extend the life of the compound. For example, the dehydrochlorinase inhibitor DMC did synergize DDT for a few generations before the resistance had intensified sufficiently to counteract both insecticide and synergist. The pyrethrin synergist piperonyl butoxide is at present doing useful work synergizing carbaryl to control the multiresistant cattle tick in Queensland.

The idea of using mixtures or alternations of two different insecticides to prevent or delay resistance developing to either is an old one, but when it was tested empirically with DDT and malathion applied to laboratory colonies of houseflies and bedbugs, and with chlordane and malathion on a colony of the German cockroach (Burden et al. 1960), it turned out that two resistances were developed instead of one. Each compound seems to improve the residual inheritance of the supporting genome to favour the development of resistance to the other. There was an example where a DDT-resistance gene allele led to enhanced susceptibility to another insecticide, but the species (*Drosophila melanogaster*) was important only to geneticists and the other compound, phenylthiourea, was a very weak insecticide. An example of negative correlation of cross-resistance has been reported between OP compounds and the formamidine chlordimeform in a strain of the two-spotted mite *Tetranychus urticae* in which the OP-resistance was due to a mutant ChE (Dittrich 1969); and another example was found in the same species between OP compounds and formetanate, a carbamate insecticide structurally related to chlordimeform (Steinhausen 1968). But the two-spotted mite has proved itself entirely capable of developing chlordimeform-resistance, as also of developing carbamate-resistance.

A quarter-century ago, when resistance was considered to be polygenic, the geneticist J.F. Crow (1952) calculated that a longer mileage for two chemicals would be obtained when the second was not substituted until after the first had been used for quite a number of generations. Eight years later, Crow (1960) conceded that mixtures might have a place for use against cases of monogenic inheritance, but considered that as the residual concentrations decreased in the field there was a danger of selecting simultaneously for two resistances. Apart from the inconvenience of using mixtures, including obtaining state and federal clearance for each such innovation, it does seem that as a general rule each compound should be run out for the entire effective life allowed it by the target arthropod species, and then replaced before it has reached the point of a control failure.

It is the role of susceptibility tests to find this point when and where it is reached. Based upon taking a sample of the insects themselves, the test eliminates the extraneous factors of formulation,

poor application and weather. These tests have been standardized and published, not only to encourage their use, but also to ensure that the tester is speaking not only to himself but to the entire entomological profession. Among the 12 tests developed by the World Health Organization, all of them are energetically used because kits of equipment to perform the tests are made available at cost; moreover, a report form ensures that the results are collected, banked on a computer, and the LC_{50} figures disseminated. For the 4 test methods developed by the Entomological Society of America and the 12 tests developed to date by the Food and Agriculture Organization, similar evidence that they are being widely used and collected is awaited.

A standard test, widely used, provides its own scale of values so that every investigator does not need to have a normal strain with which to compare his suspect populations. A systematic mapping of the results obtained can show where the insect is developing resistance to the insecticide in different parts of the world, as exemplified by the results of the WHO tests on *Culex pipiens* larvae, or by those of the special FAO survey on resistance in stored-product pests recently completed by Champ and Dyte (1976). Since it is where the growing season is long and insecticide use is high that resistance first develops in agricultural pests, tropical and semitropical regions provide forewarning to entomologists in the temperate zone; Canadians look to California to show them what they can expect in 10 years' time. An even more pressing need is for the same approach on a survey or geographical basis to be taken within individual countries or individual states within federal republics. Resistance first rears its ugly head in certain places; in fact the HCN-resistance of scales remained confined to certain citrus orchards in California, DDT-resistant codling moths in Ontario were restricted to certain orchards and cyclodiene-resistance in the western corn rootworm took several years to spread from its initial appearance in southeastern Nebraska.

For the husbanding of our resources and making the most of our limited arsenal of compounds, these first appearances in indicator trouble-spots must evoke two responses. First, the remedial insecticide chosen in our cross-resistance studies must be substituted in the trouble-spot. It is a wise

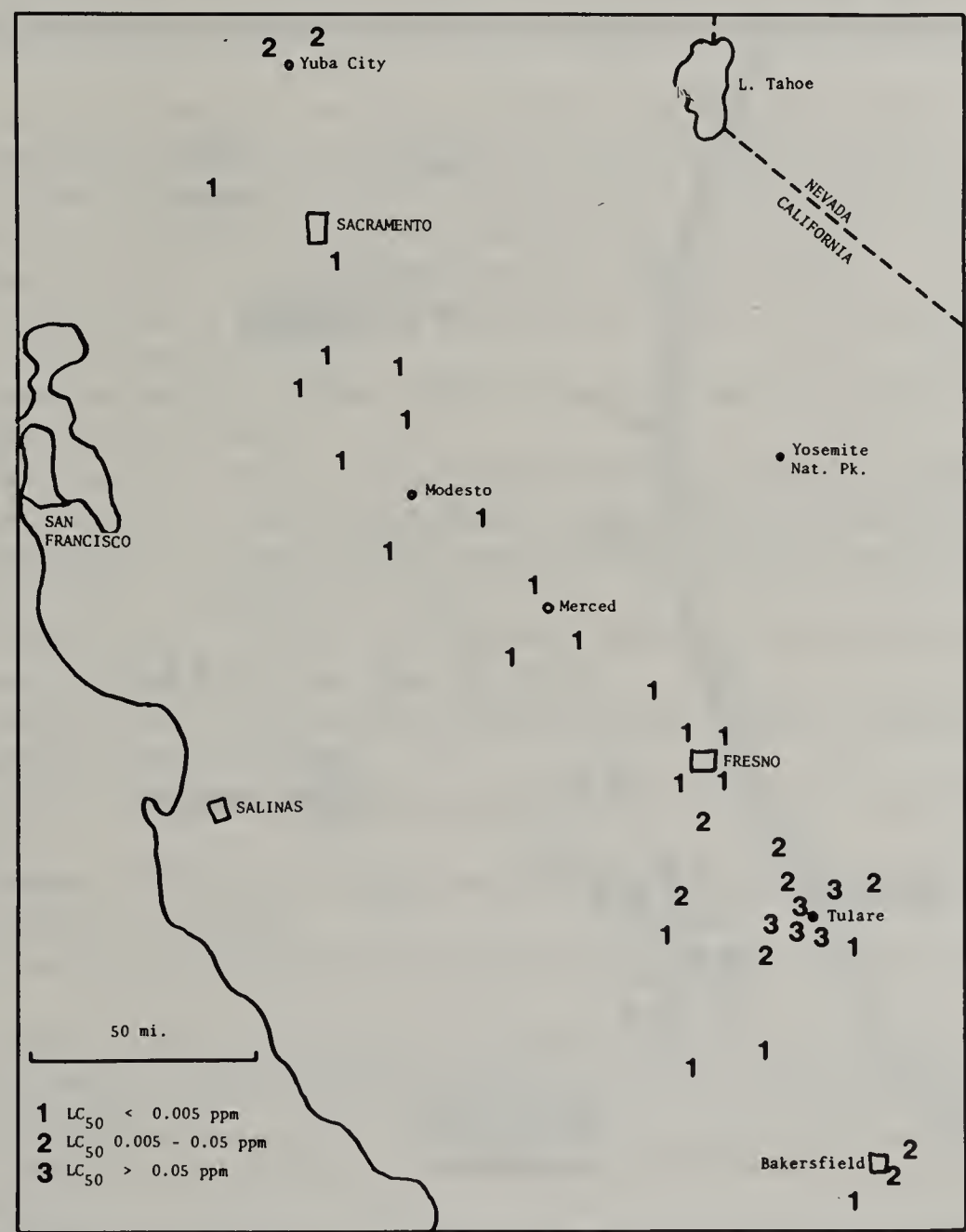


Fig. 4. — LC_{50} levels of parathion for *Aedes nigromaculis* larvae in the central valley of California (after Brown, Lewallen and Gillies 1963).

policy always to have a second-string insecticide waiting in the wings, e.g., WHO has methyl-dursban in mind should Abate fail against the larvae of the *Simulium* vector of onchocerciasis, and chlorpyrifos for use where *Culex fatigans* larvae becomes resistant to fenthion. Sometimes the same chemical company produces a remedial insecticide for its main product, as Geigy did with diazinon after DDT. Secondly, such substitution should not be made in the areas where resistance levels have not yet been approached, but instead a survey program of susceptibility tests must be assiduously carried out to ascertain what time remains for the original compound. In this way the most mileage can be made out of the compounds, which are not discarded until they have reached their term in those areas. For example, the levels of parathion-susceptibility in the mosquito *Aedes nigromaculis* (Fig. 4) showed Californians how they related to the trouble-spot around Tulare and how far each mosquito abatement district in the Central Valley had progressed in the acquisition of OP-resistance by larvae of this species. With the succession parathion-methyl parathion-fenthion-chlorpyrifos available to them, they could move from one to the next at the right point and thus extend the effective life of this group of OP compounds for as long a period as possible.

As in California, so in Michigan the survey approach has proved its value, in this case by mapping the LC_{50} levels to azinphosmethyl in the Phytoseiid mite predator of Tetranychid spider-mite pests of apple orchards (Fig. 5). This told Dr. Croft and his colleagues not only where they had to take measures to protect the predator-prey ratio against the effects of the azinphosmethyl applied against the codling moth, but where they could obtain OP-resistant *Amblyseius fallacis* to transfer to orchards where this predator was still OP-susceptible.

We must agree that our pesticide management in face of the insecticide-resistance factor over the past 30 years leaves considerable room for improvement as the century proceeds to its close. Undoubtedly the switch to less persistent OP and carbamate insecticides has improved matters, and so has the restraint from unnecessary insurance applications and the raising of acceptable thresholds of infestation. The diffusion of integrated-control systems which is the trend of our times will relegate

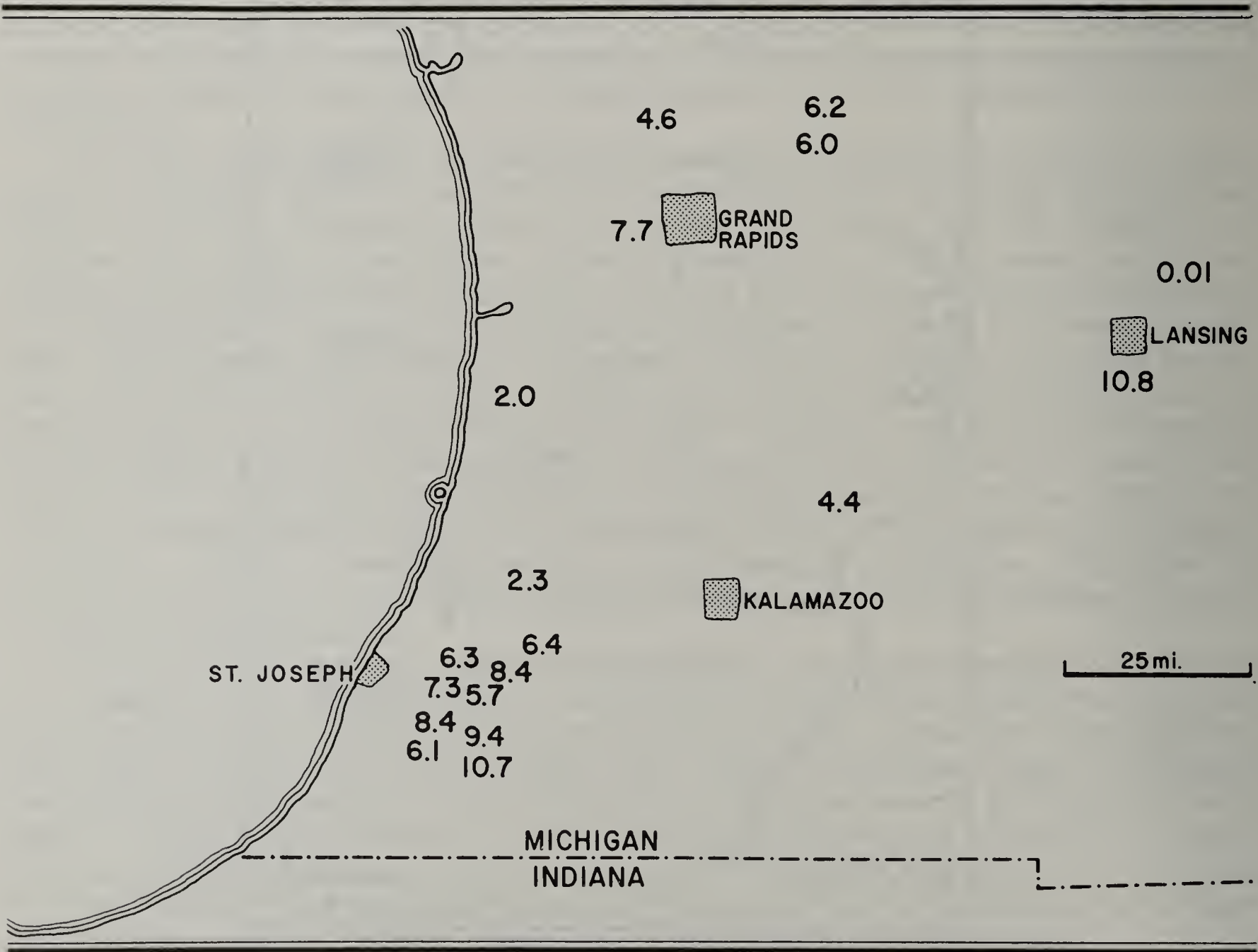


Fig. 5. — LC_{50} levels of azinphosmethyl (in lbs/100 gals) for *Amblyseius fallacis* in Michigan orchards (from Croft and Nelson 1972).

chemicals to their proper place. But we cannot escape the fact that modern agricultural production of high-quality crops now cannot avoid depending on pesticides, and that it is a first priority to ensure a wise pesticide management policy.

It seems that what is needed is not only a proper approach, but also the systematic application of method. We have been given the susceptibility tests, and more are to come; full advantage must be taken of them. It would be worth the small expenditure involved if every agricultural country or state had somewhere its own laboratory to perform the tests, along with the transport necessary for geographical surveys, maps on the walls to show the current picture, and a dedicated leader with a mind to comprehend and communicate. Too often do we have states or crop areas in which it is claimed that the resistance picture is known, but as a result of control failures and not of the forewarnings that susceptibility tests provide. In this enlightened age of pest management and infestation monitoring, insecticide-susceptibility surveillance should be an integral part, and in states or federations which have Insect-pest and/or Disease Surveys the susceptibility levels should figure as part of the subject-matter which they disseminate.

Finally, one has the strong feeling that the agricultural-chemical industry has a role to play in this phase of pesticide management. Their product, having achieved market status with so much time, effort and expense, must be protected from going over the brink of resistance for as long as possible, and conversely must not be withdrawn from use where it still remains effective. Through national agricultural chemical associations, or through international associations such as GIFAP, the industry could see to it by the various means at its disposal that the technical experts develop systems of method which will ensure the longest effective lives of the control weapons that it provides.

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